

# THE HELICINID LAND SNAIL *PLEUROPOMA EXTINCTA* (ODHNER, 1917) AS AN ENVIRONMENTAL INDICATOR IN ARCHAEOLOGY

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Land snails have long been used as palaeoenvironmental indicators in some parts of the world, but in Australia they have received little attention. Here we present new data on the geographical distribution and ecological characteristics of the helicimid *Pleuropoma extincta* (Odhner, 1917). The species is confined to the limestone outcrops of the Chillagoe Formation where it occurs abundantly both as living populations on the limestone rock and associated vegetation, and as dead shells in the litter deposits. After analysing >1,100 modern snail shells from 24 collection localities (from two major limestone regions within the formation), we argue that the sensitivity of shell growth (measured as size-correlated differences in whorl counts) to environmental moisture variation in *P. extincta* makes this species particularly suitable for palaeoenvironmental research. Differences in whorl counts of sub-fossil *P. extincta* shells from archaeological excavations at Hay Cave, in tropical northeastern Australia, are then investigated. We conclude with observations about the implications of the land snail shell sequence for the nature and timing of changes in rainfall levels during the last 19,000 years in north Queensland, and how these changes compare and contrast with existing palynological trends for the Atherton Tableland nearby. □ *Land snails, Helicinidae, Pleuropoma extincta, palaeoenvironments, archaeology, north Queensland, Australia.*

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In Australia, the use of archaeologically obtained land snails for palaeoenvironmental reconstructions is in its infancy. This is despite their frequent presence in excavated sites. Some of the problems associated with the utility of land snails in archaeological analysis were outlined by Evans (1972) and highlighted by other authors since, especially in Europe (e.g. Carter, 1990; Connah & McMillan, 1964; Sparks, 1969). Difficulties arise in two major areas: the level of knowledge about the land snail species to be used, including not only their taxonomic status but also their behavioural and ecologic traits; and the taphonomic status of the excavated samples. These difficulties are equally, if not more, applicable in the Australian sphere. This paper presents new data from north Queensland, addressing these issues so as to investigate late Quaternary palaeoenvironments along the western slopes of the Great Dividing Range, an area hitherto poorly researched.

## QUATERNARY LAND SNAILS: HISTORY OF RESEARCH

Study of gastropod molluscs from Pleistocene archaeological deposits began in the 19th century, and the possibility of using snails as indicators of past climates, local environments and as chronological indicators has been recognised since at least this time (Kennard, 1897; Lowe & Walker, 1984). As in other branches of palaeontology, much of the early work was concerned with taxonomy; relatively little attention was paid to palaeoecological considerations. By the late 19th and early 20th centuries, however, researchers in the United Kingdom began to use molluscs as palaeoclimatic indicators and as a means of dating geological events (Kennard, 1897; Woodward, 1908). During 1919 to 1939, numerous investigations followed their lead. These studies were usually published as appendices to archaeological reports. One of the earliest studies concerned the Neolithic (4,000-2,400 BC) flint mines of Grimes Graves in Norfolk, where land snails were used not only as indicators of past

landscapes, but also as evidence for the post-glacial antiquity of the mines — at that time an issue in considerable dispute (Evans, 1972).

Despite such promising pioneering works emanating from the UK (and to some degree from central Europe, particularly Czechoslovakia), to this day the analysis of land snails from archaeological deposits continues to be largely ignored in many parts of the world. Yet the argument for using land snails in palaeo-ecological reconstructions seems irresistible. Alternations of cool and warm periods, spanning various lengths of time from decades to thousands of years, are represented by soil horizons which, when not decalcified, usually contain molluscs of various species. Such changing climatic conditions during the Quaternary have been successfully identified by land snail analysis in Czechoslovakia, in much the same way that pollen has been used to define various interglacial periods. Not only can the distinction between interglacial, interstadial and glacial stages be recognised via land snails, but in many cases the fauna are sufficiently diagnostic to make relatively fine-grained climatic determinations for some periods of time (cf. Evans, 1972).

In a study with particular relevance to the current investigation, Solem (1972) documented land snails from deposits recovered in the Aq Kupruk Caves, Afghanistan. He used the general abundance of taxa in the land snail assemblage as well as size differences in the enid *Subzebrinus eremilus* (Benson, 1849), a pulmonate gastropod, to postulate prehistoric changes in moisture patterns. However, he readily acknowledged that his conclusions were restricted by the absence of knowledge about the ecology and distribution of the contemporary land snail fauna of the region and a lack of data on environmental variation within local species. In spite of these shortcomings Solem's (1972) analyses demonstrated the principle that changes in the shell-size of land snails could be used to determine past changes in environmental moisture levels.

Brief discussions of research in central Europe, the Middle East, Africa and North America can be found in Evans (1969) and Goodfriend (1992), and will not be recounted here. However, in central Europe and North America, land snail analysis is of considerable importance in various lines of Quaternary research. This is due in large part to their widespread occurrence in areas of calcareous loess (Evans, 1972).

#### LAND SNAIL RESEARCH IN THE UK: EMERGENCE OF A TECHNIQUE

In Britain, numerous regional studies have looked to land snails to investigate the timing and extent of human-induced landscape clearances from the Neolithic to the Bronze Age (Wainwright & Davies, 1995). Where land snails were once used to look at general changes in land-use patterns (e.g. Evans 1971a, 1971b for southern England), they are now being used for much higher resolution mapping of archaeological landscapes, typically at scales of about 35-80km<sup>2</sup> (e.g. Allen 1997, in press). Several factors have contributed to this. Land snails are abundant in many types of depositional contexts (including oxidised sediments); these are usually identifiable to species; and they are visible in the field, thus allowing preliminary assessments of local depositional environments (Porch, in prep.). Moreover, their appeal is also directly related to a fundamental limitation of pollen research in the UK, where an absence of peat and linnet deposits from the large tracts of chalk and limestone in southern, central and eastern England renders pollen analysis inappropriate (Evans, 1972). Pollen analysis until recently has been able to reveal virtually nothing about the environmental and ecological history of the chalklands (but see for example Seaife, 1995; Sharples, 1991). This is particularly unfortunate given the importance of such environmental settings to settlement and agriculture during prehistoric and Roman times (Evans, 1972). In contrast, palaeoenvironmental research based on land snails has enabled conclusions to be drawn on the nature of people-land relations for various periods in prehistory, including the timing of landscape clearances, the onset of agricultural practices, and the emergence of intensified settlement systems (Evans, 1972). The thrust of Evans' own work shows that ecological information can be gained from land snails with which patterns of land-use change can be addressed. Given these research foci, it is common to find in the archaeological literature discussions of land snails and the presentation of data included under captions such as "Evidence for the environment and farming economy". This is particularly so when sites such as barrows (burial mounds), pits, hillforts, pastureland and ploughzones are considered (Allen, 1995a).

It has also been recognised for some time, largely from the results of pollen analysis, that

many parts of Britain which are today open country were once forested. The East Anglian Breckland and the North York Moors are classic examples, the former having been cleared by Neolithic people some 3,000 BC, the latter during the Bronze Age by around 1,550 BC (Evans, 1972). In view of this, it has generally been assumed that the chalk and limestone upland regions were likewise once forested, having suffered a similar history of forest clearance through the actions of prehistoric farmers. By undertaking land snail analysis, landscape clearance dating as far back as the 4th millennium BC has been confirmed. As a result, it is now thought that few, if any, parts of the British Isles can today be thought of as entirely natural (Evans, 1972).

The Bucksdon Barrow site at Basingstoke, Hampshire, provides a good example of how changing frequencies of molluscan faunas with distinctive ecological affiliation can be used to identify changes in patterns and intensities of land use. An excavated section through a series of silts and mixed deposits suggested the clearance of deciduous woodlands during the Late Neolithic to Early Bronze Age. This clearance was associated with pre-barrow features and a cremation pit. Subsequently, short-grazed grasslands became established during the Middle to Late Bronze Age. By the Iron Age, the site had become overgrown by long grasses and shrubs (indicating very little or low pressure land-use) followed by intermittent arable and pastoral activity, resulting in erosion of the barrow monument (Allen et al., 1995). Consequently, molluscan evidence indicated to the excavators that major changes had taken place in systems of land use at Basingstoke since the late Neolithic, and that these changes could be divided into a number of well-defined demographic, settlement and economic systems.

#### LAND SNAIL ANALYSIS IN AUSTRALIAN ARCHAEOLOGY

Australian archaeological site reports typically include site descriptions, vertebrate faunal lists and a detailed evaluation of stone artefacts, while rarely making even a passing note of land snails. They are rarely identified even when their presence is noted, and are rarely incorporated in ensuing discussions (David & Stanisic, 1991). To illustrate this point: in SE Australia, almost all non-marine molluscan analyses have been qualitative and peripheral to the main objectives which are generally geomorphological or

palynological in emphasis (Porch, in prep.). This is somewhat surprising given the attention often paid to palaeoenvironmental indicators such as pollen from archaeological sites. It is doubly so given the high profile of land snail research in archaeology in the UK, where most of Australia's first generation of professional archaeologists were trained in the 1960s.

#### BIOGEOGRAPHY OF AUSTRALIAN LAND SNAILS AND THEIR SUITABILITY AS PALAEOENVIRONMENTAL INDICATORS.

A key biological feature of terrestrial molluscs that makes them useful in climatic reconstruction is their sensitivity to environmental moisture regimes. They have not evolved totally effective structural means to prevent water loss and desiccation is their greatest enemy. This characteristic makes them especially relevant for such studies in Australia where climatic drying (with shorter intermittent wet periods) since the Miocene has been an overriding force in determining the distribution of the biota. Such climatic changes were particularly prevalent in the Quaternary when they occurred in greater rapidity (Galloway & Kemp, 1981; Kemp, 1981; Nix & Kalma, 1972).

Biogeographic analyses of Australian land snails (Bishop, 1981; Stanisic, 1994a; Solem, 1992a, b; Pokryszko, 1996) stress the post-Miocene drying of the continent as a basic factor in the evolutionary processes that have led to contemporary distribution patterns. Reasons for this have a broader ecological basis than purely snails 'drying out'. Moisture, to a large extent, also determines the distribution of vegetation systems (Webb & Tracey, 1981) so it is not surprising to find strong correlations between distribution of land snails and certain vegetation communities; particularly rainforests in eastern and northern Australia where the majority of land snail species occur (Solem, 1991; Stanisic et al., 1994; Stanisic, 1998). Such relationships with vegetation are evident not only at the community (=guild) level but also in the geographical distribution of individual species (Solem, 1991; Stanisic, 1997c, 1998). These trends are perhaps best illustrated by the current distribution of the Charopidae, a Gondwanan family that established a close relationship with rainforests during the late Cretaceous when mesic forests were more widely spread (Stanisic, 1990).

The ecological bond between land snails and rainforest is predicated on convergent habitat preference since ecological conditions that

favour the growth and persistence of rainforest, particularly high and stable moisture availability, and eutrophic soils, are also those favoured by terrestrial molluscs. For land snails, rainforests also provide shelter and food. In most cases, the present-day restriction of land snails to suitable patches of rainforest vegetation is absolute (Stanisic & Ingram, 1998) though in a historical sense these distribution patterns should be viewed as temporally dynamic (Stanisic, 1999).

Hence from a biogeographical perspective land snails are useful for determining the vicariant shattering and isolation of mesic habitats when conditions were dry and hostile. They are also useful indicators of historic dispersal routes that became available to a wide array of organisms when conditions were moister, and thus more favourable to the movement of wet-adapted organisms (Stanisic & Ingram, 1998). From an archaeological viewpoint, they would appear to be ideal candidates for palaeoenvironmental reconstruction.

**ADVANCE AT A SNAIL'S PACE.** So why have land snails been so rarely used in Australian archaeological studies? Kershaw et al. (in press) suggest that palaeoenvironmental research based on land snails in Australia to date, has been limited by inadequate ecological and systematic knowledge. The shortcomings in taxonomic knowledge seem to be borne out by preliminary analyses of land snail diversity in eastern Australia (Stanisic, 1994a). Since the late 1970s considerable descriptive work has been completed on land snails of the Kimberley region, central Australia and South Australia (see Solem, 1992a and accompanying references), but much remains to be done elsewhere. Several detailed regional surveys of land snails by Stanisic (1994a, 1997c, 1998) in eastern Australia demonstrate more fully the extent of these shortcomings. In southeastern Australia, Smith & Kershaw's (1979, 1981) checklists of Victorian and Tasmanian land snails form the basis of knowledge for this region, however, even these are not based on comprehensive survey work.

Nevertheless pioneering studies using these animals in palaeoenvironmental reconstruction have been attempted. David & Stanisic (1991) reported a Holocene (and possibly terminal Pleistocene) land snail sequence from Echidna's Rest, an archaeological site in north Queensland and interpreted variations in the relative

abundance of mesic and dry-adapted taxa in terms of changes in regional moisture regimes.

In a study of land snail remains relative to local environments for the past 35,000 years at Warreen Cave, southwest Tasmania, N. Porch & J. Allen (pers. comm.) argued the snails indicate environmental changes reflecting regional climatic change rather than exclusively local factors.

In a second Tasmanian study (N. Porch pers. comm.) a long sequence of land and freshwater molluscs from Pulbeena Swamp, northwestern Tasmania suggests that palaeoenvironmental trends based on pollen and ostracod sequences are supported by the molluscan sequence.

Notwithstanding these studies, the limited use of land snails in Australian archaeology is regrettable when it is realised that in many parts of Australia, other palaeoenvironmental data do not appear suited to addressing archaeological questions. Many palaeoenvironmental records are founded on pollen sequences obtained from places tens or even hundreds of km from archaeological sites.

**OTHER CONSIDERATIONS.** There are two major differences between the UK and Australia in this type of research. Firstly, in the UK people have been directly responsible for massive changes in vegetation communities since the Neolithic, principally through agricultural practices. Human impacts on the landscape were extreme to the point that most climate-induced changes were dwarfed by comparison. Consequently, major changes in molluscan assemblages (Allen, 1992, 1995a) can be directly attributed to human activities. This is not the case in Australia, where climate still is a major controlling force behind both vegetation and land snail changes. While anthropogenic fires in Australia could be considered to have affected environments in a similar way as human clearance in the UK, the protected nature of limestone outcrops in Australia has significantly limited the impact of fire in these environments.

Secondly, high levels of molluscan diversity in Australia over-rides abundance. This is well illustrated by the 222 Wet Tropic species known in northeastern Queensland (Stanisic et al., 1994), as against 200 for the British region as a whole. Stanisic (1994a) recorded individual southeastern Queensland sites yielding in excess of 40 species. This allows for an organisation and interpretation of species based on their environmental associations (e.g. wet vs dry



adapted [David & Staniscic, 1991; Staniscic, 1994a]) in Australia. However, given limitations in sampling methodologies as practised in Australia, where sediment samples are sieved through wire mesh of various sizes and only the fractions caught in the mesh are kept and hand sorted for land snail shells, most very small species are by-passed and therefore ignored. Procuring and processing land snail samples from sieved excavated sediments will result in the non-collection of snails smaller than the wire-mesh (David & Staniscic, 1991) which may be critical to the level of interpretation placed on analyses. As this paper aims to show, variation in shell size of particular species, no matter how small, can provide palaeoclimatic information that may over-ride issues based on biodiversity.

**RESEARCH METHODOLOGIES.** Two major analytical methods have been applied in palaeoenvironmental research based on fossil land snails. The first, a qualitative approach, uses a taxon's modern ecological requirements to make statements about the environment of sub-fossil assemblages (Goodfriend, 1992). In general, shells can be extracted from ancient deposits and identified to species or genus. By attributing ancient shell assemblages to their nearest present-day ecological analogues, where species composition is known to be governed by climate and local habitats, some idea of past environments can be obtained (Lowe & Walker, 1984). This methodology follows procedures outlined by Evans (1972), and has recently been characterised as standard (Clcal & Allen, 1994; Allen & Wyles, 1993).

The second, a quantitative approach, uses absolute numbers or the relative abundance of particular taxa to interpret palaeoenvironments (Goodfriend, 1992). The total number of molluscan species (living and extinct) in Britain is not more than 200, and fewer than 50 of these can generally be expected in terrestrial sites (Evans, 1972). When changing proportions of represented taxa are investigated through time, it is common to divide species into ecological categories: woodland vs. shade-loving, intermediate vs. catholic, open-country vs. closed woodland, disturbance-sensitive vs. disturbance-tolerant species (Evans, 1972; Lowe & Walker, 1984). O'Conner (1988) suggested the addition of a fifth category — wet terrestrial — after studies of molluscs as indicators of slums and ditches highlighted their benefits to the history of settlement sites in wetland areas, although Robinson (1988) is more specific in

taxonomic and ecological terms. In these contexts, the usefulness of such ecological categories to the study of past people-land relations is well illustrated by the chalkland block of Malling, Cliff and Caburn. Here, the molluscan sequence has been sub-divided into phases of mature deciduous woodland with dense leaf litter, to woodland clearance and localised ground disturbance, and finally to fluctuating pressures through a grazed, dry grassland (Allen, 1995a, 1995b).

**CONCEPTS AND DIFFICULTIES.** Evans (1972) noted that practical difficulties fall into two main categories: stratigraphic and ecological. In the former, variations in the horizontal and vertical distribution of land snails in soil or sediment profiles may skew death assemblages in a way not truly reflective of past populations. For example, snails may occur on rock surfaces, among trees and leaf litter, or at varying depths underground. This results in the presence of different but contemporaneous species of land snails at different vertical levels, a potential problem often accentuated by the activities of worms and other invertebrates known to significantly disturb soil profiles (David & Staniscic, 1991). At death, snails on or above the ground accumulate on the ground surface through gravity, while those buried under the ground remain *in situ*. The physical, chemical and biological soil processes acting on this signify that the 'subfossil' assemblage (including that extracted for analysis) is distinct from the 'death' assemblage, and one further stage removed from the 'living' population (Evans, 1972).

Studies from southern Britain have highlighted processes where sediment profiles have been altered, eroded or obscured to such an extent that 'stratified' data may no longer reflect real prehistoric settlement patterns (Allen, 1994). For example, the erosion of fine soil particles by sheetwash and small rills has often resulted in the regular removal of the silt, fine sand and small stone fractions of soil profiles. The effect of this in areas of soil loss has been to artificially concentrate evidence of specific types of human activity along the upper slopes. Areas of deposition tend to show a reduction in the density of such evidence on or near the ground surface, especially where total burial has taken place. Under more energetic erosion regimes, the removal, travel and physical smashing of evidence is possible (Allen, 1991, 1994).

Previous alternating, perhaps rotational farming regimes and subsequent erosional events through valley systems have been suggested as one explanation for a paucity of Neolithic and early Bronze Age settlement in Wiltshire (Evans, 1972).

Interpretations of erosion events through land snail research have been possible given that flushes of terrestrial sediments into river and/or lake systems can be identified by the presence of non-aquatic shells and sediments within a soil profile (Evans, 1972). The relative abundance of individual species of land snails within a community is partly controlled by hereditary factors congenital to those species. Some taxa, such as *Vertigo pygmaea*, are seldom abundant, irrespective of the suitability of the habitat; others, such as *Carychium tridentatum* and *Discus rotundatus*, are often prolific. Thus, ratios between species are to some extent a function of patterns of reproduction and survival (Evans, 1972). The shells of particular species of snail also vary in their ability to resist physical and chemical destruction. Hence thin-shelled taxa, such as *Oxychilus*, tend to be more readily damaged or destroyed than more robust shells, such as *Cepaea*. Some shell apices, notably those of *Pomatias elegans* and *Clausilia*, become enlarged by the accretion of calcium carbonate, and often remain in the soil for very long periods of time. The ability of some shell species to withstand both chemical and mechanical pressures during and following burial may thus cause artificial stratification down a soil profile (Evans, 1972). These issues highlight the need to include both an adequate assessment of snail behaviour and a discussion of the taphonomic status of excavated samples for each species analysed. Taking this into account, palaeoenvironmental reconstructions based on species composition or abundance in fossil assemblages depend ultimately on a knowledge of ecological factors controlling species distribution and abundance among modern land snails (Goodfriend, 1992).

#### ENVIRONMENTAL SETTING OF STUDY AREA

Northeastern Australia is perhaps best known for the Wet Tropics World Heritage Area, a region described as possessing great biological significance in terms of species diversity and endemism. Unlike this humid belt, however, most ecosystems in the region are seasonally stressed by drought. Their research profile,

however, does not match their geographic prominence. As Gillison (1987) noted, the distribution and ecology of vegetation surrounding the Wet Tropics World Heritage Area are poorly known. Rainforest, as defined in Australia, covers a whole range of floristically related, closed canopied communities (Webb & Tracey, 1981). These communities include not only the floristically diverse and structurally complex types requiring high rainfall, but also small patches of semi-evergreen and deciduous monsoon forests and vine thickets (Kahn & Lawrie, 1983; Winter et al., 1987).

In wet coastal areas complex mesophyll or mesophyll vine forest dominate lowlands and lower mountain slopes. Mesophyll vine forests also occur at altitudes of up to 800m on basalt soils where soil fertility is particularly favourable. However, patches of sclerophyll vegetation can occur within these rainforest massifs, generally but not exclusively where rainforest development is inhibited by poor or excessive drainage and regular disturbances (Kershaw, 1994). These vegetation patterns are replaced progressively by notophyll and microphyll vine forests, and eventually simple microphyll vine-fern thickets with increasing altitude and by notophyll vine forest with decreasing rainfall. West of the ranges there is a rapid change from rainforest to open forest as the rainfall declines sharply due to the rain-shadow effect of the mountains. This usually occurs above 600m with a transition band of tall open forest extending continuously for about 360km from Mount Halifax in the south to Mount Windsor Tableland in the north. Further west towards the Gulf of Carpentaria, eucalypt forests are drier and stunted. In this area, semi-deciduous vine thickets with relatively small and restricted distributions occur. Generally they are found in locally moist and fire shadow niches. The vine thickets that occur on the limestone outcrops of the Chillagoe Formation which encompass two major karst areas (Mitchell-Palmer and Chillagoe-Mungana) are typical.

Dry vine thickets can also occur in environments very similar to surrounding sclerophyll vegetation (Hiscock & Kershaw, 1992) and in the south, a few small patches of low, semi-deciduous, dry monsoon forest endure, scattered in an arc extending southeast from Chillagoe (Bell et al., 1987).

The Mitchell-Palmer and Chillagoe-Mungana limestones, towards the northern end of this

TABLE 1. Rainfall figures for Mitchell-Palmer (mean rainfall readings taken at Palmerville for years 1889-1998, and at Bellevue for 1957-1998).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Palmerville mean (mm)	260	259	183	49	16	12	5	4	8	19	61	158
Bellevue mean (mm)	225	207	161	30	17	8	1	6	6	15	72	156
Palmerville mean no. rain days	17	18	15	7	3	3	2	1	2	3	6	11

limestone arc, are geographically isolated from each other by the Walsh River and extend from just north of the Palmer River near Palmerville Station, to northwest of Almaden in the south (Fig. 1). In both areas the climate is basically semi-arid but highly seasonal. Vegetation on these limestone outcrops, where there is shelter from fire, is deciduous, microphyll vine thicket. Fensham (1995, 1996) denoted these vine thickets as a floristically distinct group restricted mainly to limestone karst. The relatively closed canopy of the vegetation cover and the highly dissected micro-topography of the limestone karst provide a wide range of moist, shady micro-environments favoured by land snails. Within each of the two areas individual outcrops are isolated by eucalypt woodland communities which are devoid of limestone.

The vine thickets on these limestone outcrops and their associated pediments are largely fire-protected. Fire appears to have been a feature of the Australian dry tropics landscape for a considerable period of time (Kershaw, 1985), but its influence has increased in intensity with the arrival of Aboriginal people more than 40,000 years ago (Singh et al., 1981) and Europeans in the last 150 years. This has complicated interpretations of environmental change based on the analyses of vegetation assemblages from pollen studies (Kershaw, 1985, 1986). However, the limestone substrate forms a natural barrier and protects the fire-sensitive vine thicket vegetation and the associated land snails. Hence climatic interpretation based on analyses of variation in shell characteristics from these environments should be relatively free of the influences of fire.

Limestone outcrops in each of these locations has been mapped by the Chillagoe Caving Club (1982, 1988, 1990) and the following brief assessments of local environments are based on these publications.

*Mitchell-Palmer.* The Mitchell-Palmer limestones outcrop in a series of towers running roughly in a north-south line from north of the Palmer River to the Mitchell River in the south (Fig 1). Tower height varies, but exposures up to 150m above the surrounding landscape have been recorded (Fig. 2). Mean annual rainfall at Palmerville in the north is 1034mm; at Bellevue Station at the southern end it is 901mm, in both cases with more than 90% of the rainfall coming in the period November-April. Mean annual rain days at Palmerville = 88 (Table 1). Evaporation and transpiration exceed precipitation for eight months of the year, with the area experiencing a marked winter deficiency of water for plant growth. Towers are higher than those at Chillagoe-Mungana and include massive scree slopes (Chillagoe Caving Club, 1988).

*Chillagoe-Mungana.* The limestone bluffs of the Chillagoe-Mungana region are situated in a rough northwest to southeast line extending from Rookwood Station in the north, through Mungana and Chillagoe to slightly northwest of Almaden in the south (Fig. 3A). The individual towers vary from narrowly circumscribed outcrops to expansive, relatively high limestone masses (Fig. 3B). Rainfall at Chillagoe-Mungana is less than in the Mitchell-Palmer region, with the annual average around 850mm, most of which occurs between November and April (Table 2). The entire Chillagoe-Mungana region, from its northwestern to southeastern ends, can

TABLE 2. Rainfall figures for Chillagoe-Mungana region (from north to south) (Chillagoe mean mm from 1902-1998; Rookwood mean mm from 1961-1997; Almaden mean mm from 1972-1998, Chillagoe mean rain days for 1979-1982).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Rookwood mean (mm)	225	210	130	21	13	8	2	4	4	12	64	148
Chillagoe mean (mm)	219	213	141	30	14	11	4	4	5	15	56	130
Almaden mean (mm)	226	193	137	54	16	8	5	4	8	18	67	132
Chillagoe mean no. rain days	16	15	9	5	3	2	1	1	1	2	4	8



FIG. 1. Map of northeastern Australia showing areas >600m ASL; and distribution of limestone karst towers of the Mitchell-Palmer and Chillagoe-Mungana regions indicating locations of archaeological sites and other places mentioned in text.



be treated as a single climatic region, with variation through space being minimal. This is well illustrated by the similarities in mean annual rainfall levels for Rookwood (850mm), Chillagoe (854mm) and Almaden (852mm). Similar patterns also exist for mean monthly rainfall levels (Table 2).

The number of annual rain days in the Chillagoe-Mungana region is also less than in the Mitchell-Palmer (e.g. average for 1979-1982 = 65). A number of the limestone towers contain caves which are today the focal points of local tourism (Chillagoe Caving Club, 1982; Robinson, 1982).

**PALAEOENVIRONMENTS IN NE QUEENSLAND.** Most of what we know of Quaternary palaeoenvironments in northeast Queensland comes from pollen research along the eastern seaboard and the convection-affected Great Dividing Range a few kilometres to the west. Few investigations have been made in the rainshadow area to the west of the Range, an area which covers most of north Queensland where the magnitude of environmental change can be expected to be significantly less than on the Atherton Tableland and coastal regions where coastal processes are strong. Kershaw's work at various sites from the Atherton Tableland, some 150km to the southeast of Mitchell-Palmer and Chillagoe-Mungana — at Lake Euramoo, Quincan Crater, Bromfield Swamp, Strenckoff's Crater and Lynch's Crater — has revealed a series of pollen sequences covering the last 215,000 years. More recent work at the ODP 820 offshore site (Kershaw et al., 1993), Isabella Swamp, Kings Plains Lake, Garden Creek Swamp, Napabina Swamp and Barwon Swamp in the Laura region some 100km to the northeast of Mitchell-Palmer (Stephens & Head, 1995), Lake Carpentaria 500km to the west (Torgensen et al., 1988) and Ngarrabullgan some 75km to the southeast (Butler, 1998) have revealed further pollen data for palaeoenvironmental reconstructions, especially for the Holocene period. Other relevant research from tropical northern Australia and the near Pacific include works on past sea levels (Hopley, 1983; Chappell et al., 1983), oxygen isotopes on corals (Aharon, 1983), ancient charcoals and woods (Hopkins et al., 1993), cheniers (Chappell, 1982; Chappell et al., 1983), lake levels (Bowler, 1983; Torgensen et al., 1988), dunefields (Galloway et al., 1970), cave sediments (Hiscock, 1984; Hughes, 1983) and simulation studies (Nix & Kalma, 1972). Together, these studies enable us to present the

following palaeoenvironmental reconstructions for the last 40,000 years of northeastern Australia.

**40,000-38,000 BP.** This was a relatively wet phase, although both absolute and relative rainfall levels were probably lower than they are today. Records from Lynch's Crater indicate that the araucarian vine forests that had dominated much of the last glacial period as well as the previous glacial, were displaced by pyric sclerophyll forests dominated by *Eucalyptus*. An order of magnitude increase in charcoal peaks at Lynch's Crater coincides with this change. Given that there is little evidence for substantial climatic change around this time, Kershaw (1985, 1986) has used this change as indicating the onset of human activity, particularly burning of the landscape. The regional nature of the *Araucaria* decline is indicated by a similar sequence of events at both Lynch's Crater and the offshore ODP 820 record (Kershaw et al., 1993).

**38,000-25,000 BP.** Temperatures were low, but increased slightly from c.36,000 to 30,000 BP, then decreased to their lowest value sometime after 25,000 BP. Geomorphological investigations indicate that lake levels were higher than they were before c.26,000 BP. Bowler (1983) argued that this lake-full stage indicates greater rainfall (a humid expansion) around 28,000 to 26,000 BP. This is probably best explained by increases in summer rainfall. Lakes then began to contract c.25,000 BP, indicating the advent of maximum glacial activity (Bowler, 1983).

**25,000-17,000 BP.** The time of the Last Glacial Maximum was characterised by low effective and absolute precipitation, described as about one-third of today's levels. This was probably caused by a mixture of exposed continental shelves (drier air masses), decreased oceanic temperatures (decreased convection), and a severance of warm ocean currents from northern Australia (decreased convection) (Hopley, 1983).

**17,000-8,500 BP.** Effective and absolute precipitation remained low. After the height of the last glacial maximum sometime between 13,000 and 10,000 BP, however, conditions were slowly reversed. Levels of atmospheric humidity and precipitation increased with the initial flooding of the Gulf of Carpentaria c.11,000 BP, but it was not until c.8,000 BP that warm ocean currents flowed across Torres Strait (Hopley, 1983). The spatial distribution of charcoal fragments in and around present-day rainforests

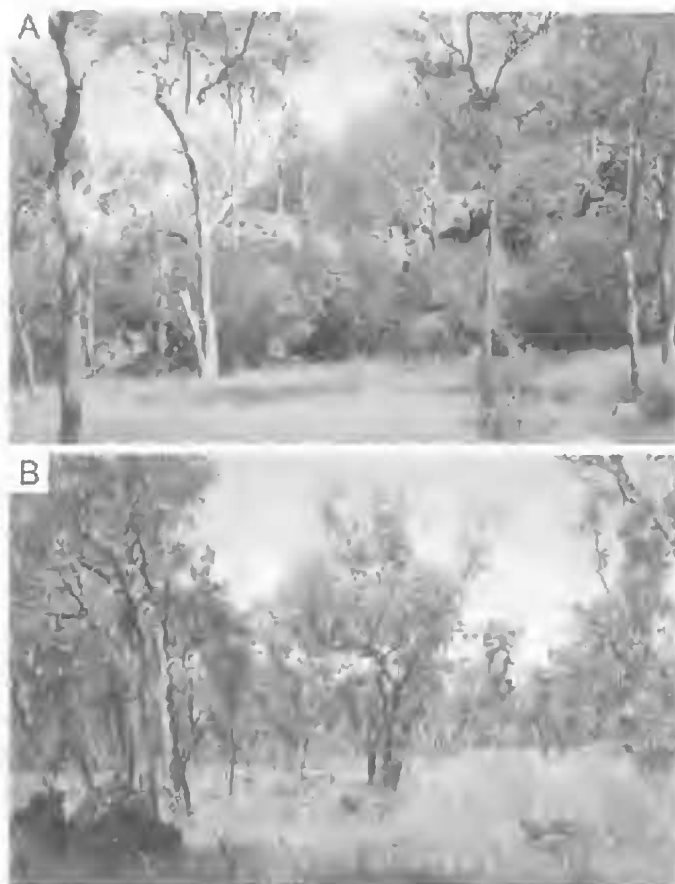


FIG. 2. Mitchell Palmer limestones. A, limestone tower and associated vine thicket; B, eucalypt woodlands surrounding the limestone towers.

suggests that the *Eucalyptus* expansion and rainforest displacement reached their maximum extents during the period 13,000–8,000 BP (Hopkins et al., 1993). By c.8,500 BP, both effective and absolute precipitation had increased to levels similar to today's: temperatures were probably also similar to those of today.

**8,500–3,000 BP.** This is a period of high rainfall and high temperatures. By 8,500 BP, both effective and absolute precipitation had increased to levels higher than today. Temperatures were probably similar to today. By 6,500–5,900 BP, rainfall attained levels nearly five-times those of the terminal Pleistocene on the Atherton Tableland. Explanations include an opening-up of the northern and eastern continental shelves, the creation of an eastern high energy window, the presence of convection as a result of warmer ocean currents, increased air and oceanic

temperatures and higher seas levels. Around 6,000 to 5,000 BP, sea levels were similar to today's (and possibly slightly higher), and micro-atoll and reef formations began to appear — much of the eastern continental shelf experienced reef growth and the formation of micro-atolls by around 5,000 to 4,000 BP (Hopley, 1983). The latter closed the high-energy window, slightly decreasing rainfall levels and thus effective precipitation. Palynological and sedimentary evidence from the crater lakes suggest that fire frequencies had declined and rainforest species recolonised certain areas, with rainforest achieving its maximum extent around 6,500–5,900 BP. This coincided with an increase in *Elaeocarpus* relative to Cunoniaceae and *Rapanea* pollen values. From surface sample data, *Elaeocarpus* pollen has its major representation in lower altitude forests. Bioclimatic analyses of taxa from Lake Euramoo suggest that summer temperatures may have been higher than today's, while rainfall continued to be high during winter (Hiscock & Kershaw, 1992).

**3,000 BP–present.** Following a lowering of absolute and effective levels of precipitation around 3,000 BP, northern Australia attained its present climatic regime. There is also

an indication from Ngarabullgan that vegetation changed shortly after 2,000 BP from forests with a relatively dense overstorey to more open forest with a grassy understorey, and that charcoal levels in sediments increased, perhaps in response to the increased fire susceptibility of that forest type. Dry rainforest was probably present, at least in patches, due to the occasional representation of *Araucaria* pollen. From this interpretation it is speculated that the change to more open communities facilitated the onset of swampy conditions or lake formation due to increased erosion and sediment input from more exposed soil surfaces (Butler, 1998). This is in accord with the suggestion of Stephens & Head (1995) that swamp formation was widespread in southern Cape York Peninsula after 2,700 BP (but see Hiscock & Kershaw, 1992).



FIG. 3. Chillagoe-Mungana limestones. A, small outcrops; B, large tower; C, litter zone.

There is some evidence for the onset of El Nino/Southern Oscillation (ENSO) after ~7,000 BP. The evidence for changing ENSO influences in Australia is evident in past fire, drought and erosion regimes and in the stress- and disturbance-tolerant vegetation that indicate more variable climates (McGlone et al., 1992: 435). This evidence has been argued to indicate colder, drier summers than previously between 5,000 and 3,000 BP, approximating present conditions. McGlone et al. (1992) conclude that early Holocene climates were more stable than for the mid and late Holocene, pointing to 'either a much reduced amplitude of the ENSO fluctuations, or to a change in the extra-tropical expression of ENSO due to different climatic boundary conditions. It is unlikely that typical ENSO cycles were a major factor in Australasian and South American climates before about 7,000 BP, and they only began to exercise their present strong influence beginning at 5,000 and fully developed by 3,000 BP'.

In short, the record for the last few thousand years emerges as problematic. This is particularly

evident given that Stephans & Head (1995) have proposed that water levels have been more reliable in the last 2,700 years, while Hiscock & Kershaw (1992) nominate driest Holocene conditions occurred between 2,600 and 1,400 BP. The disturbance of upper sediments within pollen sites is suggested as one possible explanation (Stephans & Head, 1995). However, such discrepancy more likely implies not a single discrete period of changed environmental conditions but increased climatic variability during the last 3,000 years, with short periods of decreased wet season rainfall (Lees et al., 1992). As noted above, some studies (McGlone et al., 1992; Shulmister & Lees, 1995) have gone further, arguing for the onset of ENSO from the mid Holocene. Australian droughts generally coincide with El Niño events, a relationship most consistent over eastern and northern Australia, while prolonged, heavy rainfall and consequent floods accompany the reverse cycle known as La Nina. The general effect of these events is to increase rainfall variability across the continent and through time (McGlone et al., 1992).

# INVESTIGATING PALAEOENVIRONMENTS IN NORTH QUEENSLAND VIA LAND SNAILS

While some land snail taxa, such as *Vertigo* spp. in Europe (Evans, 1972) and *Subzebrinus eremitus* in Afghanistan have been used as indicators of past changes in moisture levels, comparatively few detailed studies have ever been made of the response of particular shell characteristics to specific climatic or environmental factors (see Goodfriend, 1986 for summary).

David & Stanisic (1991) used the total land snail assemblage from an excavation at Echidna's Rest, tropical northeastern Queensland (Fig. 1), to make broad-scale regional interpretations of environmental change in the Chillagoe region, and also emphasised that individual species may yield useful micro-environmental data. Much of our understanding of the alternation of wet and dry phases since the late Pleistocene has been gained from pollen analyses of sample cores from lacustrine environments relatively close to the eastern seaboard (e.g. Kershaw, 1970, 1971, 1975, 1976, 1985). However, while this pollen work has revealed extremely long and more or less continuous sequences, some spanning hundreds of thousands of years, palaeoclimatic and palaeoenvironmental conditions for some periods of time and for some modern biogeographic zones are better understood than others.

One deficiency that is particularly problematic for archaeologists is a paucity of such data for the period 17,000 to 10,000 BP. This poorly understood period of time is compacted in the pollen sequences studied so far, particularly at the major pollen site of Lynch's Crater (Kershaw, 1974, 1976, 1994). Elsewhere in Australia, the palaeoenvironmental evidence is clear and consistent, indicating sustained rainfall rises after the last glacial maximum at various times after 17,000 BP. In northeastern Queensland, however, the existing pollen evidence for this period, while of poor temporal resolution and dubious stratigraphic quality, implies that annual rainfall levels may not have increased until ~13,000, and perhaps even as late as 10,000 BP. Indeed, terminal glacial aridity may have been greatest around 13,000 BP (Kershaw, 1994). A determination of the timing of increased rainfall in this region has major implications for archaeological reconstructions. For example, Lamb (1996) and David & Chant (1995) argued

that people were restricted to a few sources of surface water during the dry season in the Chillagoe region during the last glacial maximum, broadening their territories and altering systems of land use as conditions became wetter and biomass increased after ~17,000 BP. Evidence for such changes in cultural behaviour is evident at Fern Cave near Chillagoe, and possibly at Hay Cave in the Mitchell-Palmer limestone zone to the north where large, permanent and apparently long-standing springs can be found. However, if rainfall levels did not begin to increase until well after people had already abandoned these places and/or broadened their lived horizons, alternative models of change in settlement behaviour – specifically site and regional land use – and cultural dynamics relative to environmental conditions would have to be considered. Unfortunately, appropriate pollen sites are rare in these regions, and sedimentation rates across the landscape are generally very slow, rendering suitable palaeoenvironmental indicators outside of caves hard to find.

The shells of land snails from archaeological excavations within this region, particularly those which span the period from the last glacial maximum to present, would appear to be capable of providing the information necessary to address such questions – especially if sufficient numbers could be recovered for size analyses. Their presence within caves and rockshelters, where sedimentation is usually varied but more or less continuous, affords us the possibility of obtaining stratified sub-fossil assemblages covering relatively long periods of time. Land snails could thus act as an independent test for existing palaeoenvironmental trends, as well as perhaps also providing a finer level of detail than pollen analyses are capable of achieving. Pollen sequences are often limited to evidence of genus or higher-order changes in community composition. Vegetational changes affecting the species or sub-species often fail to register in the pollen record. This is particularly problematic in Australian semi-arid conditions, where *Eucalyptus*, *Acacia* and *Melaleuca* tend to predominate the upper storeys. Under such circumstances, changes in species composition are rarely identifiable from the pollen record, unless a genus or higher-order taxonomic change also takes place. However, some environmentally sensitive species of land snails may be able to overcome this limitation. The Echidna's Rest study identified the helicimid *Pleuropoma*



*extincta* (Odhner, 1917), which is a prosobranch gastropod, as a likely candidate for such analyses.

Prosobranch gastropod land snails, such as *P. extincta*, are more appropriate environmental indicators than pulmonates. They have an open pallial cavity rather than a closed lung, suggesting that these species are much more liable to respond to environmental moisture changes than is the case with pulmonates (Solem, 1991). In the latter the lung can be used as a 'water-bag' for storing moisture, thus potentially ameliorating the effects of dry climatic phases, both spatially and temporally. This greater sensitivity to changes in environmental moisture regimes could be expected to reflect in more easily detectable size changes in the shells of these animals. The underlying rationale is that as rainfall patterns and microenvironmental humidity levels vary, so will activity periods which determine growth rates.

Hence the usefulness of *P. extincta* in palaeo-environmental reconstruction is dependent ultimately on two main factors: firstly, the capacity to show that this species does in fact respond to environmental moisture change (in time and space) in a way that can be easily measured and analysed; and secondly, the ability to recover sufficient undamaged material from an archaeological or palaeontological excavation with an extended and finely calibrated temporal sequence. The latter problem involves not only questions of site preservation, but also of excavation methods.

**PLEUROPOMA EXTINCTA: ECOLOGY AND DISTRIBUTION.** In many land snails moisture-related responses are reflected in changes in shell patterns which can be measured. These include size, whorl number and shell thickness, although in the latter the correlation has yet to be thoroughly studied (Goodfriend, 1986). While other factors — such as temperature, insolation, the availability of calcium and population density — are also known to affect shell size, moisture appears to be the best documented factor (Goodfriend, 1986) and has been the basis of several detailed studies (Tillier, 1981; Gould, 1984) which suggest that it perhaps is a critical factor in determining both size and shape differences within species and between populations. Considering the acute moisture sensitivity of land snails, such a conclusion would seem appropriate. However, given the relative lack of studies in this sphere

and the inconclusive nature of some, it is not possible to accept the universality of the moisture-size relationship and each case must be assessed separately. It also needs to be kept in mind that though the size of shells is determined by whorling pattern, shells can become large in two ways: few large-sized whorls or many small-sized whorls (Gould, 1984). However, a strong positive correlation between size and whorl count may also indicate that size increase is purely a function of whorl count increment without any appreciable change in whorl size. Hence, determining the shell parameter which will be most useful as an index of moisture levels also becomes a crucial consideration.

**LAND SNAILS IN SEASONAL ENVIRONMENTS.** Environmental moisture-related variation in the shell size of Australian land snails has been reported by Solem & Christensen (1984) for camaenids from the vine thickets of the Kimberley and inferred for a number of non-camaenids from other seasonal environments in tropical northern and northwestern Australia (Solem, 1982; 1984). In each of these cases the implication was that variations in shell size correlated with differences in whorl numbers of adult shells and that they were not merely due to variations in overall size wherein large shells result from larger animals with larger whorls and vice versa. Furthermore, Solem (1991) suggested that shell-size variation in populations of *Pleuropoma walkeri* (Smith, 1894), a helicimid from the vine thicket patches of northwestern Australia, may also be a reflection of differences in local moisture conditions, although no analysis was undertaken. This latter inference has significant implications for using *P. extincta* in fine-grain palaeoenvironmental reconstruction.

Reasons for the size differences in the shells of the land snails from these monsoonal (= seasonal) environments relate directly to the nature of the climate and the specific adaptation of the local snails to this climate (Solem & Christensen, 1984; Solem, 1988). These land snails have the capacity to vary in adult shell size because of variations in the length of feeding activity available during growth from juvenile to adult (Smith & Stanisic, 1998). This feeding activity is related to intensity and duration of summer rainfall ('the wet'), and since these snails appear to reach adulthood synchronously at the end of their second wet season (Solem, 1982; 1984), maturity can lead to adults with different whorl numbers depending on the quality of the growing

seasons. However, it also needs to be noted that while rainfall results in growing activity, this response is not always a simple function of annual rainfall or annual number of rain days. Rather, land snail activity periods during and after significant 'activating' rain events vary according to the complexity of local environmental conditions, which include such factors as vegetation cover, topography and geology (Solem, 1988).

The Chillagoe-Mungana and Mitchell-Palmer limestone outcrops (Fig. 1) are part of this archipelago of seasonal environments and receive most of their rainfall in a relatively short time during summer (see above).

The land snail faunas of limestone areas in eastern Australia are comparatively rich when compared with the snail fauna of the surrounding non-limestone areas (Stanisic, 1994; 1997a,b). However, while the diverse nature of the fauna in some of these areas has been documented (Stanisic, 1997c), many of the taxa have yet to be formally described. The land snails of the limestones of the Chillagoe Formation are no exception. Odhner (1917) described the first species from Chillagoe and since then only a few extra species have been added (Iredale, 1937, 1938). Their classification and distribution are summarised in Smith (1992). Stanisic (1997d) briefly detailed and illustrated the land snail fauna of the Chillagoe-Mungana limestones, including undescribed species, and drew attention to its diverse make-up of widespread and locally endemic taxa. The equally prolific Mitchell-Palmer land snails are largely undocumented, though they are well represented in the collections of the Queensland Museum.

These two limestone areas share a number of taxa, including *P. extincta*. This species displays shell size variation across the range of its occurrence (Stanisic, unpubl.). *P. extincta* has also been recovered from archaeological excavations at Hay Cave, towards the northern end of the Mitchell-Palmer limestones (Fig. 7). Radiocarbon dates associated with cultural remains from this cave suggest a temporal sequence covering the last ~19,000 years at least, a time period which spans a number of major wet/dry climatic phases in the region.

These circumstances provide an opportunity to examine the extent of shell variations in recent *P. extincta* and to see whether these have palaeo-environmental implications.

*Pleuropoma extincta* (Odhner, 1917). The shell of *P. extincta* is small (adult size: diameter 2.3-6.6mm, height 2.0-5.4mm), top-shaped and sculptured with numerous spiral cords; the periphery is angulate, there is no umbilicus and the shell is relatively thick (Fig. 4). Its small size and relatively thick walls make *P. extincta* shells capable of withstanding relatively high levels of chemical and mechanical weathering, an important consideration when investigating buried sequences. *P. extincta* is comparatively widely distributed (N-S approximately 175km) in the Einasleigh Uplands Biogeographic Region, but it is environmentally restricted (Stanisic, unpubl.). It appears to live exclusively on the limestones of the Chillagoe Formation (Fig. 1). The species was mistakenly recorded from a tiny patch of vine thicket in the Mt. Mulligan area, northeastern Queensland by Stanisic & Ingram (1998). While the Mt Mulligan population is superficially similar to *P. extincta*, recently obtained anatomical details show that it is a different species (Stanisic, unpubl.). *P. extincta* is an obligate vine thicket dweller (Fig. 2A) and has not been recorded from the more expansive eucalypt forest/woodland communities which dominate much of this region (Fig. 2B). It is also absent from the vine thickets growing on the massive lava flows which occur in the surrounding countryside, such as at Undara and Kinrara to the south. The latter habitats are occupied by another, undescribed species of *Pleuropoma* (Stanisic, unpubl.). Present-day distribution of *P. extincta* is the result of long-term, climatic changes which have also affected the distribution of vine thicket communities (Stanisic, unpubl.). Because of their enhanced ability to retain ground moisture, vine thickets associated with the limestone pediments act as refugia for *P. extincta* and other micro-organisms during dry phases. *P. extincta*'s current restriction to these habitats is indicative of its past and present sensitivity to regional and local moisture regimes.

*P. extincta* lives chiefly under strewn limestone talus, on leaves and bits of timber in the litter and on the trees which grow on these outcrops. It may also occur on the limestone rock where it seals itself to the karst surface in the many cracks and crevices. Compared with most other land snails on these limestones, it is present in very high numbers. *P. extincta* is not subterranean but may occur around the entrance of caves. It does not burrow, an important consideration when analysing subsurface, sub-fossil assemblages. Its

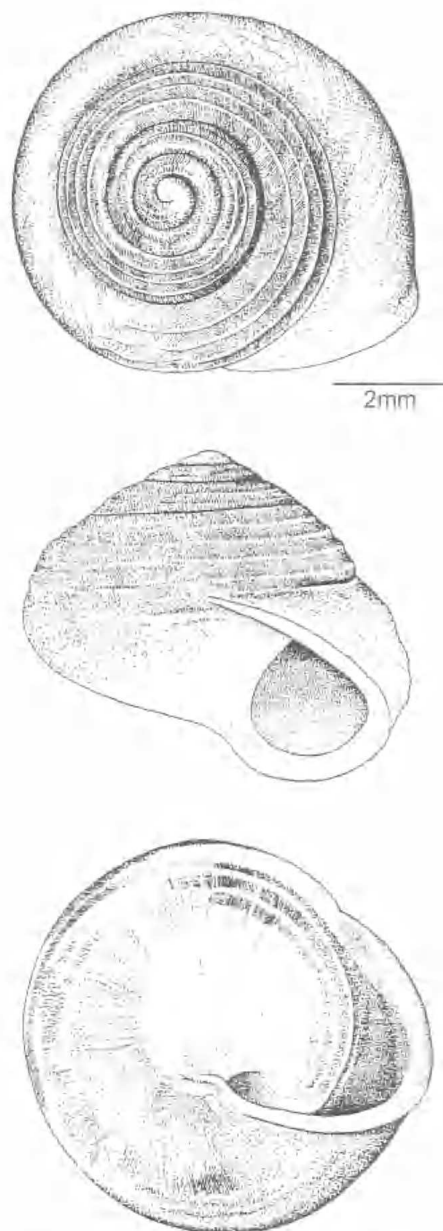


FIG. 4. Shell of *Pleuropoma extincta*. [A. Francis].

presence in great numbers along drip points within caves is probably a result of the removal of finer, surface sediment particles by percolating water, concentrating larger particles (including snail shells) in exposed pockets. Because of their large numbers in living populations and the alkaline nature of the environment, dead shells also accumulate in the litter in great abundance (Fig. 3C).

## MATERIALS AND METHODS

Recent specimens of *P. extincta* came from the collections of the Queensland Museum (QMMO). Methods comprised hand-collecting specimens and specimen-containing leaf litter from various limestone outcrops, including the ground surfaces of cave entrances and interstitial spaces between rocks and boulders on talus slopes. The shells were subsequently separated from the leaf litter by hand-sorting in the laboratory. Shells retrieved from leaf litter represented the accumulation of several years of dead individuals. The ability to sample land snails *post-mortem* greatly enhances their utility in environmental interpretation.

Preliminary analysis of samples involved separation of individuals into three categories; adult or juvenile, based on the thickness of the outer-lip (peristome), and unclear according to the degree of coating of calcium carbonate. Each sample category was counted, totalled and labelled. To facilitate measurement 10 adult *P. extincta* shells were placed at a time on the stage of a calibrated dissecting microscope (Zeiss 475052-9901) and observed by reflected light under  $\times 12$  magnification. The parameters measured were whorl count, height and diameter. Of those that were partially broken or damaged, it was only possible to measure one or two of the three variables. These damaged specimens were also counted and labelled.

Shell height was measured from the apex to the base of the aperture, and diameter covered the lateral span of the body whorl. These observations were recorded to the nearest 0.05mm. Measurements beyond 5.00mm were performed with a dial calliper (Mitutoyo 505-667 D20F), accurate to 0.01mm. Calculation of whorl number was coordinated by aligning the origin of the whorl pattern at the apex in the vertical position and counting to the nearest eighth rotation (Solem, 1976).

**STATISTICAL ANALYSIS.** The mean value for each parameter within each outcrop unit sample was calculated to a single standard deviation. In this way, statistical comparisons of parameters from different sites were possible. In each analyses the range of measurements was noted for each character.

For convenience of data presentation and interpretation, variations within shell characteristics are presented as scatter-graphs of diameter vs. whorl count, height vs. whorl count and height vs. diameter. Such statistical analyses

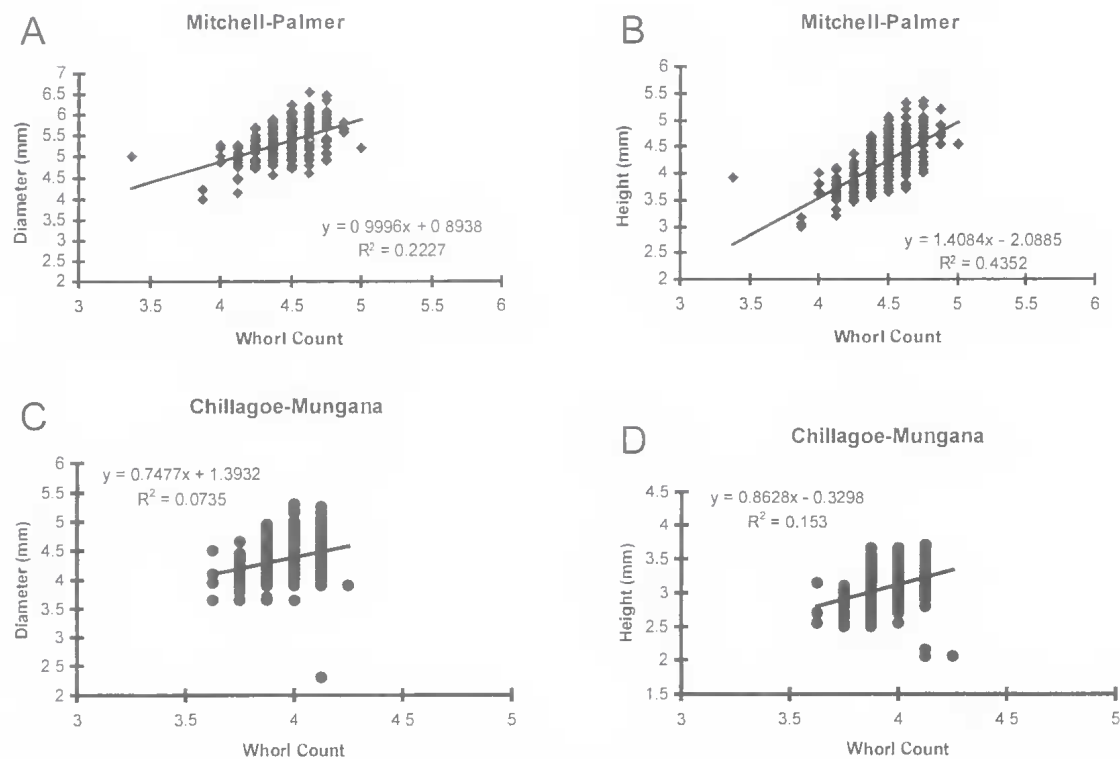


FIG. 5. Surface collections (control samples), *P. extincta* statistics (with simple regressions). A, whorl count versus diameter (mm), Mitchell-Palmer; B, whorl count versus height (mm), Mitchell-Palmer; C, whorl count versus diameter (mm), Chillagoe-Mungana; D, whorl count versus height (mm), Chillagoe-Mungana.

were first undertaken for each individual sample set (i.e. samples from individual limestone outcrops). In order to investigate spatial patterning in shell height, diameter and whorl count within a regional framework, adult data were pooled into a combined Chillagoe-Mungana dataset, and into a Mitchell-Palmer dataset. To describe and quantify the relationship between the parameters, and determine the strength of any possible correlation, a simple regression analysis and associated equation is provided for each graph.

In addition, to allow for an understanding of the relationships between the parameters for the entire study and determine the correlation strengths at this scale, all regional data were combined on a single graph. This technique therefore used all measured variables in the one analysis. Here, the regressions were second-order polynomial to account for the presence of two regional populations (Chillagoe-Mungana and Mitchell-Palmer).

#### RECENT PLEUROPOMA EXTINCTA

*Analysis of shell variation* (Tables 3-5). Average largest shells and highest average whorl counts occur among the Mitchell-Palmer material (Fig. 5A,B).

When the Mitchell-Palmer and Chillagoe-Mungana areas are treated together, whorl count depicts strong positive correlation with height and diameter (correlation coefficient ~0.72-0.83; Fig. 6A,B). When each region is treated in isolation, however, the strength of this relationship is not as evident (Fig. 5A-D), with the correlation coefficient failing to exceed 0.44. This latter poor correlation is also evident when each collection area was analysed as a separate

TABLE 3. Range of variation in *P. extincta* (mean, sem and range).

Locality	No. of specimens	Height (mm)	Diameter (mm)	No. of whorls
Chillagoe-Mungana	602	3.075±0.224 (2.05-3.70)	4.344±0.280 (2.30-5.30)	3.947±0.101 (3.625-4.250)
Mitchell-Palmer	542	4.205±0.353 (3.00-5.35)	5.361±0.350 (4.00-6.55)	4.468±0.165 (3.375-5.000)



TABLE 4. Local variation in *P. extincta* from Mitchell-Palmer area (mean, sem and range).

QM Reg. no.	No. of specimens	Mean height (mm)	Height range (mm)	Mean diameter (mm)	Diameter range (mm)	Mean whorl count	Whorl count range
MO22998	5	3.110±0.119	3.00-3.30	4.150±0.087	4.00-4.20	3.925±0.112	3.875-4.125
MO23375	72	3.844±0.019	3.45-4.20	5.179±0.226	4.75-5.80	4.377±0.159	4.000-4.750
MO23388	7	3.950±0.515	3.20-4.70	4.850±0.420	4.45-5.60	4.464±0.310	4.125-4.875
MO23584	29	4.036±0.202	3.65-4.45	4.984±0.234	4.55-5.35	4.401±0.158	4.125-4.750
MO23592	7	4.150±0.367	3.65-4.65	5.529±0.438	4.90-6.10	4.482±0.152	4.250-4.625
MO61156	208	4.148±0.249	3.60-4.85	5.285±0.243	4.70-5.95	4.468±0.134	4.125-4.875
MO61172	24	4.381±0.210	3.85-4.70	5.427±0.251	5.00-5.85	4.531±0.129	4.250-4.750
MO61191	87	4.342±0.262	3.80-5.05	5.452±0.222	4.95-5.90	4.476±0.180	3.375-5.000
MO61205	103	4.529±0.317	3.95-5.35	5.735±0.294	5.00-6.55	4.557±0.123	4.250-4.875

outcrop unit. In terms of variation, the whorl counts, diameters, and heights of shells from any one region, single limestone outcrop unit or individual collection unit appear smaller; the spread between the values becoming narrower, forming a cluster, rather than distinct linear spread, on the graph. Relating this to analytical scale, the positive correlation between whorl count and size of the shells is thus illustrated at the inter-regional level and does not arise at a more local scale. This patterning is also visible in the geographical pattern of rainfall variation, which is fairly marked at the inter-regional level, but not at a local scale. This correlation implies that the relationship between whorl count and diameter or height is likely to be extrinsic rather than intrinsic. It implies that the relationship between whorl count and diameter or height requires variation in environmental influence(s) on these variables. This is consistent with findings of strong environmental, and in particular humidity, influences on whorl growth (see above). Highest whorl counts, calculated as % of total numbers of individuals occupying various whorl count classes, shows the Mitchell-Palmer specimens to be consistently higher than those at Chillagoe-Mungana (Table 3).

**ENVIRONMENTAL INTERPRETATION.** Differences in mean shell size between the Mitchell-Palmer and Chillagoe-Mungana material correlate positively with differences in local rainfall regimes. On average the Mitchell-Palmer specimens are larger than Chillagoe-Mungana ones, which has lower average annual rainfall. Although larger shell size can result from a number of other factors, such as temperature, insolation, calcium availability, population density and soil pH, their effects were not measured. Studies elsewhere have linked some of these factors with differences in whorl

expansion rates, shell weight, diameter and height (Bengston et al., 1979; Owen, 1965). In most instances, differences in shell size were related to differences in whorl cross-section.

Goodfriend (1986) presented several hypotheses to explain the relationship between these environmental variables and adult shell size. However, in most cases the differences were in connection to the initial size of the whorls and the rate at which the whorls expanded — that is, the aperture and whorl cross-sectional area (=whorl volume). In this case, variation in aperture and whorl cross-sectional area do not represent a similar function to the number of whorls, but they are generally interpreted as representing either an adaptation for regulation of water loss, to reduce predation, or both. They are, therefore, not as dependent on the surrounding habitat (Goodfriend, 1986).

In the context of this study, the strong positive correlation between whorl count and both diameter and height in *P. extincta* indicates that size differences in this species have an affinity to variations in whorl 'count' rather than whorl 'size'. These findings coincide with the camaenid land snail growth patterns in semi-arid areas of northwestern Australia as discussed by Solem & Christensen (1984). Adult shell size in their study is seen to depend upon moisture conditions near the end of the snail's second wet season. An early interruption of moisture supply causes growth to stop at a lower whorl count and produces smaller adults. Favourable moisture conditions allow extended growth time, with cessation occurring at a higher whorl count, and producing a larger adult size (Solem & Christensen, 1984). What Solem & Christensen (1984) implied is that the regular and predictable wet season in the Kimberley region is the key to understanding the maturation pattern of its land snails. The length of

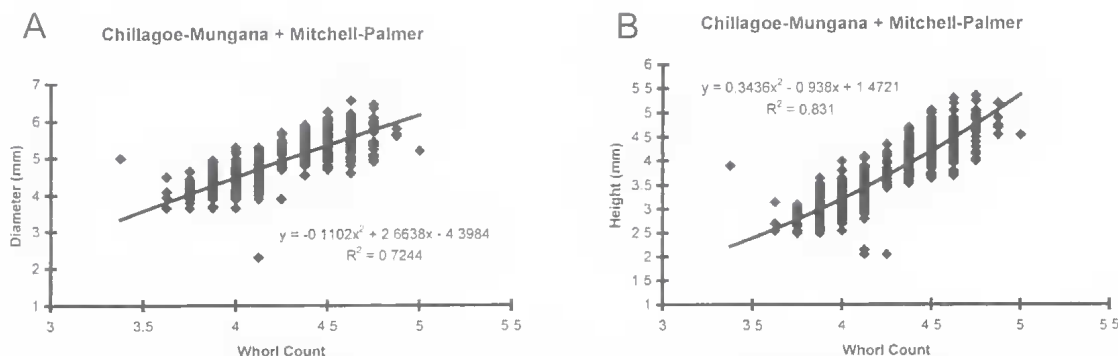


FIG. 6. Mitchell-Palmer + Chillagoe-Mungana. A, whorl count versus diameter (mm); B, whorl count versus height (mm). Regressions are second-order polynomial, to take into account the presence of two regional populations.

the wet season may vary from as little as two months on the southern fringes, to as long as six months in the Mitchell Plateau. The median wet season rainfall is only 500mm near Fitzroy Crossing and Halls Creek, but nearly 1600mm on the Mitchell Plateau. These parameters define the potential maximum length of the activity period for the snails (Solem & Christensen, 1984).

The lower number of rain days at Chillagoe-Mungana compared to the Mitchell-Palmer appears to at least partially account for the smaller-sized (= lower whorl count) snails. Given this, whorl count in *P. extincta* appears to be a useful indicator of differences in regional rainfall levels, which in turn suggests that this shell feature may also be a useful index of change in past environmental moisture levels along the limestone belt of the Chillagoe Formation. Evidence indicating the sensitivity of *P. extincta* to environmental moisture levels is strengthened through the presentation of initial findings highlighting little intra-regional variation, where each outcrop has a fairly uniform rainfall pattern. However, the most significant correlation between size and whorl count is between regions with perceptible differences in mean annual rainfall levels.

In contrast to the above, Solem & Christensen (1984) concluded that the pattern of size variation in land snails in the Kimberley region was very much a local phenomenon dependent on both moisture regimes and microhabitat. Populations of *Westraltrachia* at Wombarrella Gap differed by up to 3mm in mean adult diameter over distances of less than 100m. The small shells were collected near a single isolated boulder, and the larger specimens were taken in shaded talus

that would retain moisture for a longer period of time (Solem & Christensen, 1984).

Although the north Queensland results do not show the strong patterns of local variation seen in some Kimberley species it should be borne in mind that the recent material was mostly collected from large karst towers whose micro-topography was generally considered to be similar. There are however, tantalising indications that local influences would be worth further investigation and that outcrop size and aspect may also play a mitigating role in final shell size of *P. extincta*. For instance, material from Mitchell-Palmer sample QMMO22998 was collected from a small, low relief outcrop and has comparatively smaller whorl counts and size than others from the region (Table 4). Specimens from Royal Arch Caves, Chillagoe-Mungana (QMMO53436) displayed the largest size and whorl counts for specimens from this region (Table 5). While this limestone outcrop does not demonstrate any apparent physical differences to others from the region, the land snail assemblage does suggest that it has intrinsic differences. The large camaenid land snail, *Spurlingia praeahadra* (Odhner, 1917), occurs almost exclusively on this outcrop indicating that it probably is somehow environmentally distinctive. Further research on these aspects appears warranted because if these casual perceptions about local differences in *P. extincta* are related to local habitat differences, then the role of *P. extincta* as a useful indicator species would be enhanced.

#### APPLICATION TO AN ARCHAEOLOGICAL ASSEMBLAGE: HAY CAVE

Hay Cave is located towards the northern end of the Mitchell-Palmer limestone belt, near

TABLE 5. Local variation in *P. extincta* from Chillagoe-Mungana area (mean, sem, range).

QM Reg. no.	No. of specimens	Mean height (mm)	Height range (mm)	Mean diameter (mm)	Diameter range (mm)	Mean whorl count	Whorl count range
MO15955	9	3.067±0.224	2.70-3.40	4.411±0.204	4.00-4.65	3.931±0.110	3.750-4.125
MO19527	85	2.968±0.220	2.05-3.40	4.189±0.208	3.65-4.60	3.891±0.107	3.625-4.250
MO25996	40	3.111±0.195	2.55-3.55	4.328±0.186	4.00-4.75	3.931±0.109	3.750-4.125
MO38499	6	3.100±0.148	2.90-3.35	3.975±0.829	2.30-4.45	3.979±0.094	3.875-4.125
MO50229	15	2.823±0.231	2.50-3.40	4.173±0.171	3.90-4.45	3.908±0.088	3.750-4.000
MO50231	19	3.324±0.197	2.95-3.65	4.616±0.242	4.00-4.95	3.961±0.094	3.750-4.125
MO53325	31	3.148±0.166	2.80-3.45	4.574±0.237	4.20-5.15	3.948±0.090	3.750-4.125
MO53335	19	3.005±0.222	2.70-3.50	4.363±0.309	3.90-4.95	3.888±0.109	3.750-4.125
MO53436	25	3.452±0.154	3.20-3.70	4.910±0.194	4.60-5.30	4.070±0.063	4.000-4.125
MO53448	20	2.860±0.240	2.15-3.20	4.050±0.145	3.65-4.25	3.944±0.137	3.625-4.125
MO53551	21	3.060±0.119	2.90-3.30	4.400±0.152	4.15-4.65	3.929±0.075	3.875-4.125
MO53564	20	3.063±0.143	2.85-3.40	4.310±0.136	4.05-4.55	4.013±0.099	3.875-4.125
MO58485	220	3.116±0.184	2.05-3.40	4.386±0.216	3.80-5.00	3.953±0.089	3.750-4.125
MO58540	31	2.947±0.158	2.65-3.35	4.074±0.145	3.70-4.40	3.948±0.063	3.875-4.000
MO58547	41	2.985±0.174	2.60-3.45	4.237±0.164	3.90-4.55	3.976±0.098	3.750-4.125

Palmerville Station. Mean annual rainfall is estimated to approximate 1,034mm given its proximity to the station. It is a medium- to large-sized cave positioned at the base of a large limestone tower. The site's entrance is located at an estimated 2m above the surrounding plains. The area outside the dripline displays evidence of roof collapse in the form of numerous boulders. Boulders caused by roof-fall are also present inside the dripline in some cave chambers, but never in the central area of human occupation, where the excavation was undertaken. The cave entrance is itself not visible from the outside, as it is hidden by a thick web of vine thickets. These circumstances lead to a lack of direct sunlight reaching the cave, and consequently a relatively constant, cooler and humid internal climate.

Evidence of human activity includes a massive boulder whose edges have been flaked and numerous paintings that occur from the entrance to the very back of the cave, a distance of approximately 17m. The central part of the cave possesses soft, ashy floor deposits, signalling the presence of ancient fireplaces below ground.

**FIELD AND LABORATORY METHODS.** Hay Cave was excavated by BD and HL as part of an Earthwatch-funded project in mid 1996 (Fig. 7). The reasons for the excavation were multiple, focusing on human responses to environmental change in north Queensland during the last glacial maximum (in particular the period 21,000 to 13,000 BP). Four juxtaposed 50 × 50cm squares (test pits), forming a 1 × 1m square

matrix, were excavated. Excavation commenced near the central zone of soft ashy surface deposits where sediments appeared to be deepest (and potentially oldest) and least disturbed by animals and water. The 4 test pits were labelled M30, M31, N30 and N31. Square M30 proved to be the deepest square excavated and the focus of subsequent investigations.

Excavation methods employed ~2cm excavation units (XU) within stratigraphic units (SU). This method simply recognises that sediments have in the past accumulated progressively, at times resulting in the formation of distinct strata. Excavation units are employed during excavation because sediments of similar composition may have accumulated over long periods of time, so that a single stratigraphic unit may represent many hundreds or even thousands of years of sediment accumulation. Excavation units thus enable the excavator to sample different parts of a given stratigraphic unit, enabling an investigation of its internal structure and contents.

Major changes in sediment colour, texture and observable content at the time of excavation and section description were deemed separate SU: minor stratigraphic changes were identified as changes in sub-layers. The SU were numbered sequentially from top to bottom, with sub-layers characterised by an alphabetical letter after the SU number (e.g. SU2a and SU2b). The location of all cultural material measuring over 2cm maximum diameter and observed in situ was





FIG. 7. Hay Cave.

recorded in three dimensions, plotted on recording forms and bagged separately. The remaining sediments were weighed, dry-sieved in 3mm-mesh wire sieves and bagged for subsequent sorting. In the laboratory, this material was later wet-sieved, air-dried and sorted. Sorted sediments thus resulted in various components for each XU, including stone artefacts, bone, mussel shells, land snails and calcium carbonate ( $\text{CaCO}_3$ ) concretions. Sediment samples from the <3mm residue were collected from each XU from each square along with pH readings. Pollen and oriented sediment micromorphology samples were also collected

from the pit walls upon completion of the excavation.

**Dating.** Eight samples for radiocarbon dating were extracted from square M30. Seven of these dates were derived from charcoal; the remaining OZD-012 determination was on freshwater mussel shell. All samples were collected *in situ* from the upper two SU where sediments were relatively easy to dig. These radiocarbon dates were obtained from various parts of the square, covering much of the sequence. The charcoal and mussel shell were pre-treated for possible rootlet and carbonate contamination by the radiocarbon laboratories before dating. Sample Wk-6053 was sent to the University of Waikato Radiocarbon Laboratory (Hamilton, New Zealand). All other samples were forwarded to ANSTO (Physics Division, Lucas Heights Research Laboratories, Australia). The former date is a conventional radiocarbon determination, the latter by accelerator mass spectrometry (AMS) (Table 6).

**Microscopic and statistical analysis of excavated materials.** The segregation of materials from the excavated sediments provided a useful opportunity to identify changes in the relative proportions of components. This allowed the

TABLE 6. Radiocarbon dates from Hay Cave.

XU	Depth (cm)	Age (BP)	Lab no.
XU2	1.4	350±55	Wk-6053
XU6	8.0	660±75	OZD-006
XU12	17.1	870±65	OZD-007
XU26	46.0	2,590±80	OZD-008
XU34	64.0	3,100±60	OZD-009
XU45	91.0	13,450±150	OZD-011
XU49	102.8	13,600±180	OZD-422
XU56	118.2	19,300±140	OZD-012



quantity of deposited land snail shell to be graphed according to excavation unit. A similar method was employed to graph the frequency of  $\text{CaCO}_3$  concretions. In turn, the *P. extincta* shells were separated in an equivalent manner to the modern collections, enabling the number of specimens deposited per unit time to be calculated. Shell measurements and statistical analysis were undertaken in the same manner as employed in the modern samples. The mean whorl count, height, and diameter from each excavation unit were outlined on three graphs. Low *P. extincta* counts in some XU highlighted a need for caution in interpretation, and consequently neighbouring XU with under 10 specimens were combined to increase sample size. A third order polynomial regression was super-imposed on the graphs. This choice of regression type reflects the aim of investigating long-term environmental change, the nature of variation within the data and the possible representation of three major climatic regimes for the period in question, as informed by pre-existing palaeoenvironmental research. Trends in shell characteristics were then identified through time.

**RESULTS.** Radiocarbon determinations (Table 6) of age range from c.19,300 to c.350 years BP, and a precision of one standard deviation is given for each. All dates are in sequence.

*Deposition of sediments within Hay Cave.* There is a high incidence of land snail shells by weight (all species combined, but consisting mainly of large *Hadra* aff. *bipartita* and *Xanthomelon pachystylum*) from 13,600 BP to around or shortly before 3,100 BP (XU49-XU38) (Fig. 8). This incorporates a peak of 688.0g at XU40. Prior to this time, total shell weights are comparatively low. Above XU38, a pronounced decrease to almost negligible levels is evident, encompassing the period 3,100 BP-present (XU33-XU1). The highest incidence of  $\text{CaCO}_3$  concretions in Fig. 9 corresponds in timing with the period of peak land snail shell deposition, between 13,450 BP and 3,100 BP (XU45-XU34).

Deposition rates of *P. extincta* shells per 100 years (Table 7) reveal two major depositional regimes: one before approximately 3,100 BP (XU56-XU35) characterised by significantly low shell frequencies, and the other since 3,100 BP (XU34-XU1), when numbers are some 20-fold higher.

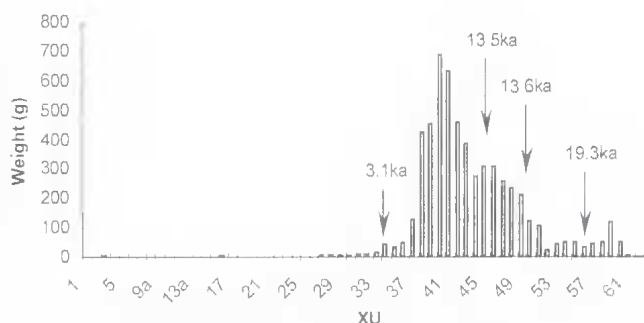


FIG. 8. Land snail shell excavated from square M30, Hay Cave: total land snail shells by XU.

*Pleuropoma extincta* at Hay Cave. A total of 295 *P. extincta* shells were recovered from excavation square M30 at Hay Cave. Most (236) are adult specimens, with 59 at undetermined stages of maturity given the presence of  $\text{CaCO}_3$  encrustation or breakages effectively removing or hiding characteristic features. Of the adult specimens, 17 were partially broken. This left 219 specimens where each of the three measurements — height, diameter and whorl count — could be made.

Mean whorl counts, heights and diameters by excavation unit at Hay Cave are represented in Fig. 10. A description of relationships is based on the shapes of the regression curves, which display similar trends but are not identical to each other. Of the three represented graphs, mean whorl counts demonstrate minor variation across the time span, indicating slight decreases from an under-pronounced peak at 13,600-13,450 BP (XU49-XU45). Values change little from about 3,100 BP (XU34) until 660 BP, after which they decline further to 350 BP (XU2) and present levels. However, variability between individual samples through the sequence is high.

TABLE 7. Deposition rates of *P. extincta* numbers per 100 years at Hay Cave (note that XU45 to XU49 were not separated as dates were within one standard deviation of each other).

XU range	No. of shells	Duration in years	No. shells/100 years
XU1 - 2	27	350	7.71
XU3 - 6	33	310	10.64
XU7 - 12	32	210	15.24
XU13 - 26	89	1720	5.17
XU27 - 34	59	510	11.57
XU35 - 49	53	10,500	0.50
XU50 - 56	1	5700	0.02

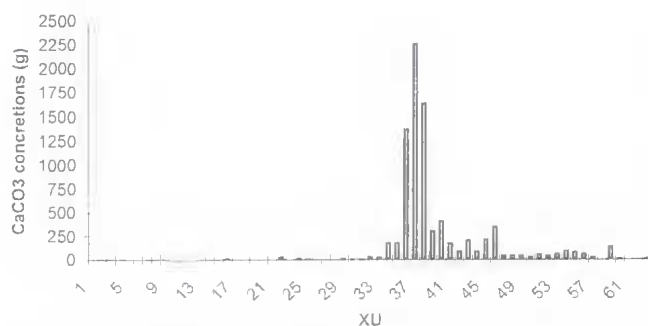


FIG. 9. Total weight of calcium carbonate concretions excavated from square M30, Hay Cave, by XU.

Mean heights show more extreme variation of the trends evident in whorl counts, expressing a greater decrease through the last 660 years (XU6-XU2) and indicating an obvious peak at 13,600 BP (XU49). This peak is followed by a marked decrease through the period 13,450-2,590 BP (XU45-XU26) and a rise to a lower peak at 660 BP.

The trend for mean diameter is similar to that for mean height. This tendency was generally expected given that height showed strong correlation with diameter in the Mitchell-Palmer and Chillagoe-Mungana control study. The *P. extincta* shells dating to 13,600 BP (XU49) correspond to peak levels, decreasing to relatively small measurements from 3,100 to 2,590 BP (XU34-XU26). Diameters rise to a second, almost equal peak through the period 870-600 BP (XU12-XU6), after which they decrease to low levels. As with mean height, variability between individual samples is high.

**DISCUSSION.** Major temporal phases can be identified from the Hay Cave fossil molluscan records via an analysis of shell sizes and whorl counts. These quantifications in turn can be linked to trends in relative frequency of land snail shells through the dated sequence. However, such comparisons also raise questions about the broader geographical applicability of existing palaeoenvironmental trends based on pollen.

The general shapes of the regression curves are likely to be reliable, given the stratified nature of the sequences which appear to possess good internal integrity. However, the degree of stretch (as opposed to the shape) of the regression curves — that is the length of each section of each curve — is dependent on the period of time covered rather than by the depth of deposits. Currently these curves have been presented by excavation unit, which basically represents depth below

ground. The last 3,100 years are over-emphasised in such curves, given peak sediment deposition rates during that time.

The early to mid Holocene period appears to be present in the Hay Cave sequence despite an absence of radiocarbon dates from this period, given the high land snail shell and  $\text{CaCO}_3$  concretion frequencies from XU45 to XU34 (Figs 8,9). However, their exact timing is uncertain, given a total absence of radiocarbon determinations for this part of the sequence.

The frequency of redeposited  $\text{CaCO}_3$  can be taken as an indicator of changing moisture regimes, given the susceptibility of limestone to solution. The greater the solubility of a substance, the greater its liability to come out of solution. Many minerals are deposited in caves as chemical precipitates, and calcite is the mineral form of  $\text{CaCO}_3$ . Although reactions are reversible, calcite is chiefly precipitated through the diffusion or 'degassing' of carbon dioxide ( $\text{CO}_2$ ) from water into the atmosphere. To describe a general reaction, seepage water, initially enriched in  $\text{CO}_2$  given the presence of soil and vegetation, becomes saturated in calcite when passing through joints in the limestone. Upon entering the cave environment with lower partial pressure of  $\text{CO}_2$  in its atmosphere than in the soil above,  $\text{CO}_2$  diffuses from dripping and flowing water and causes calcite to be precipitated out of solution and deposited. In essence,  $\text{CaCO}_3$  deposition in caves implies a supply of water and vegetation growth sufficient to enrich soil water with carbon dioxide for limestone solution. From this, calcium carbonate is observed as an inorganic indicator of high moisture levels (Jennings, 1985)

The calcium carbonate curve is matched by other proxy indicators of environmental humidity. As a biological index, the incidence of land snail shell (Fig. 8) mimics the relative frequency of  $\text{CaCO}_3$  concretions between 13,450 and 3,100 BP, an alliance related to the notion of Evans (1969) that essentially all molluscs are aquatic animals. As discussed, the habitats and behaviour patterns of terrestrial snails are largely controlled by the humidity of the environment. For example, *Hadra* aff. *bipartita*, a dominant taxon between XU45 and XU34, requires humid conditions. Observations on species in north

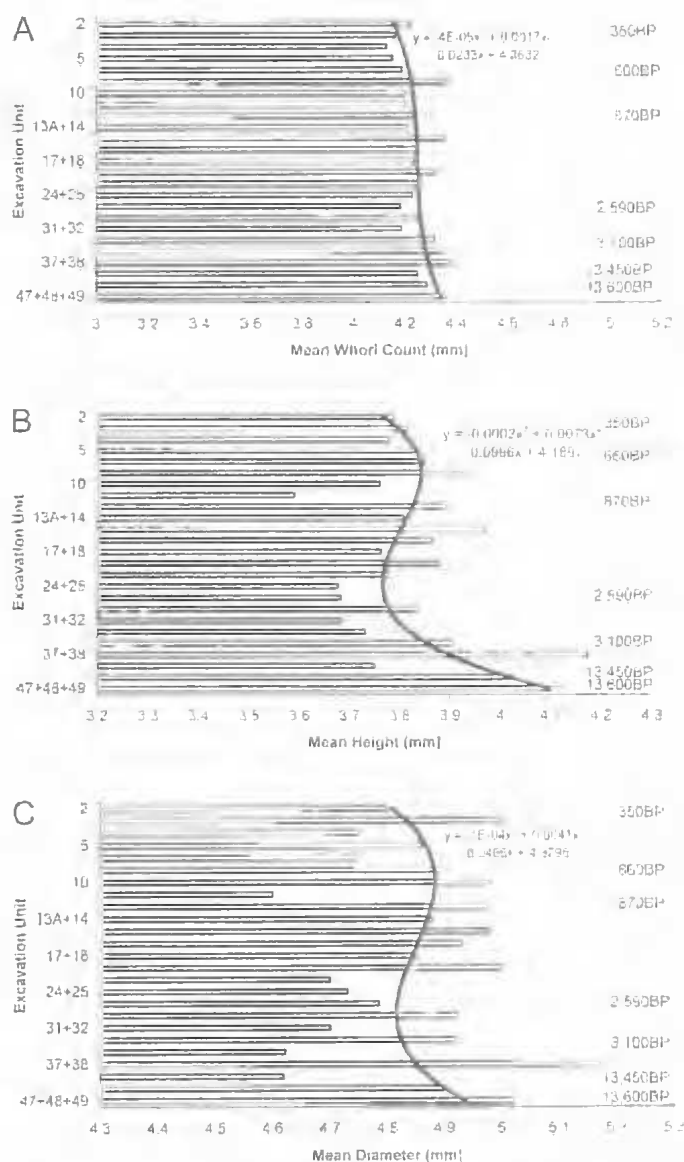


FIG. 10. *P. extincta* measurements by XI. Hay Cave. A, mean whorl count; B, mean height; C, mean diameter.

Queensland suggest that land snail activity is largely confined to the wet season, and hence there may be a relationship between the length of the wet season and number of individuals. The high shell accumulation, together with  $\text{CaCO}_3$  concretions could indicate conditions were wettest during the period 13,450 to 3,100 BP in the Hay Cave sequence, independent of *P. extincta* shell measurements. This would be consistent with high rainfall regimes during the early to mid Holocene, as informed by existing

palaeoenvironmental data from other parts of north Queensland (see above).

It is difficult to determine why an absence of radiocarbon dates exists for the early to mid Holocene. The charcoal in the Hay Cave excavation is likely to all come from anthropogenic camp fires. As David & Lourandos (1997) recognised, however, there is no simple relationship between amount of charcoal in a site and the number of radiocarbon dates obtained. In turn, the number or presence of radiocarbon dates may not be indicative of the magnitude of human occupation, as biases in the creation, recovery, and preservation of charcoal and radiocarbon dates in a sequence or in a region are more likely to critically affect results. Biases may skew the date curve, and thus potentially falsify the common assumption that human occupation will produce more deposited carbon, even if the relationship is not strictly proportional. At Hay Cave this is well illustrated by the continued presence of burnt bone, shell and earth in the purported early Holocene levels where no radiocarbon dates have yet been obtained and charcoal is very sparse. We argue that such an absence of charcoal in these layers is not due to its original absence, as evident in the ample cases of burnt materials in those layers. Rather, charcoal has probably been removed post-depositionally, either as a result of high humidity levels rendering the charcoal fragile and susceptible to mechanical damage, or through other, as yet undetermined means.

This issue is currently the subject of further investigations by BD and HL.

However, increases in deposition rates of all cultural materials during the late Holocene indicate that broader factors are also at work. Land snail shell deposition rates, as calculated by numbers of *P. extincta* per unit time, show that shell frequencies were low within this early Holocene period, in comparison to the late Holocene. This may mean that terminal Pleistocene/early Holocene conditions were dry

rather than wet. If this was the case, this trend would question the validity of the above interpretations of  $\text{CaCO}_3$  and total land snail concentrations as evidence of a wet phase. However, we would rather argue that the low frequency of *P. extincta* (and other small) shells during the early Holocene is due to their very small size and their inability to frequent soggy ground surface conditions, as was probably the case at the time (see above). If rainfall levels were significantly higher during the early to mid Holocene as it was during the terminal Pleistocene, which appears to be the case from the pollen evidence to the east, moisture regimes may have breached the upper thresholds for very small land snails (<6mm in size). This is consistent with the predominance of large species of shells at Hay Cave during this time, including the wet-adapted species *Hadra* aff. *bipartita*.

While the issue of continuous vs. intermittent deposition of sediments at Hay Cave is beyond the ability of this paper to resolve, its resolution may be important for a better understanding of palaeoenvironmental trends in the region as a whole. If in fact the sediment accumulation rate at Hay Cave is a function of the presence of Aboriginal people in the environment rather than of natural phenomena, compared to the late Holocene, the formation of only 27cm of deposit between  $13,450 \pm 150$  and  $3,100 \pm 60$  BP would be consistent with lower levels of human occupation than subsequently. For Hay Cave, what these late Holocene sediment increases mean in terms of human behaviour remains uncertain, but it is possible that, like Mitchell River Cave, Hearth Cave and Mordor Cave also in the Mitchell-Palmer region (David & Chant, 1995), intensive occupation did not begin until the late Holocene, and before this time the caves may not have been extensively used as living sites.

### CONCLUSIONS

This paper has focused on techniques of land snail shell analysis and their usefulness to palaeoenvironmental reconstructions for the period spanning the Last Glacial Maximum to present in north Queensland. In the process, a wide range of themes have been covered, including: history of Aboriginal land use (archaeology); plant biogeography; geological and climatic processes; and land snail ecology and taxonomy, from historical as well as modern day perspectives.

It is salutary to recall here that the presence and value of molluscs in archaeological deposits was

recognised more than a century ago, and yet their detailed investigation has only recently begun in Australia. Considering the rapid development of palynology in the last 30 years, and together with the great potential of Mollusca to inform us on historical trends in both climatic and environmental change, it is perhaps rather surprising that such a state of affairs should have arisen (Evans, 1969). At present, nonetheless, most Australian studies of fossil land snails require taxonomic and ecological investigations of modern land snails to be undertaken before palaeoenvironmental research can be conducted. Once this necessity is accepted, a wealth of potential palaeoenvironmental information is available from fossil land snails. As is apparent from their abundance in buried deposits, their ability to be identified to species level, their sensitivity to moisture regimes, and their strong affinity with vegetation type, *P. extincta* snails have demonstrated their value as proxy indicators of palaeoenvironments in semi-arid landscapes. It is likely that both *P. extincta* and other species of land snails can be used for palaeoenvironmental research in other environmental zones in various parts of this continent.

An existing body of regional palaeoenvironmental evidence has provided a context for the Hay Cave land snail data. Although the quality of these data is variable, marked but variable community and taxon responses to glacial/interglacial cycling is apparent. The northeastern Queensland environment has been a dynamic and diverse system (or rather, interconnected set of systems) where the gross composition of the vegetation fluctuates in relation to cyclical changes in climate and sea level. The humid tropics region of northeastern Queensland has provided a substantial and detailed history of rainforest and rainforest-sclerophyll interactions via pollen analysis at a number of sites on the volcanic Atherton Tableland. These pollen sequences indicate that during the late Quaternary, the Tableland was subject to significant environmental variability. It has been proposed that similar changes in climate have been experienced throughout northern Queensland, although changes may not have been entirely synchronous nor of equal degree in all places.

Complementing these established palaeoenvironmental studies, we argue that *P. extincta* shell whorl counts are also dependent on moisture regimes and thus reflect fluctuations in



mean annual rainfall. Based largely on pollen research, last glacial maximum has been interpreted, independently of land snail research, as being a period of dry conditions. This was followed by a period of increased (to peak) precipitation during the early to mid Holocene. In its turn, this period of time was itself followed by an effective drying. These major changes in moisture regimes can be expected to have affected the spread, floristic structure and complexity of semi-deciduous vine thicket in north Queensland. Given *P. extincta*'s restricted distribution to such vegetational communities and their sensitivity to moisture, the broader applicability of our extant knowledge of palaeoenvironmental (including palaeoclimatic) trends can be tested and refined. Thus, the most important changes in the *P. extincta* record since 19,300 years BP are the relative increases in precipitation starting at 13,000 BP and a relative lack of whorl count variation at Hay Cave. Results at Hay Cave, to some degree, differ from those of the Atherton Tableland models based on pollen analyses, which have so far largely failed to address their relevance for regions to the west of the Great Divide. Far from constituting negative evidence, in contrast to the Atherton curves, the Hay Cave data suggests a more stable rainfall regime through time, although directions of change are consistent with the Atherton trends. As Head & Stuart (1980) concluded, this type of pattern has the potential to help quantify the limits within which climate systems operate.

The lower magnitude of environmental change west of the Great Dividing Range suggested by this study now warrants further investigation. Given the current status of land snail research, multidisciplinary studies would aid in assessing the extent of this phenomenon, as well as testing the accuracy of land snail models in palaeoenvironmental reconstructions. The need for the application of additional tests in such research was briefly demonstrated in this paper by a consideration of the formation of  $\text{CaCO}_3$  concretions in cave sediments, and of depositional frequencies of all land snail species. A more extensive investigation of these issues may provide a better impression of past moisture levels and palaeoenvironmental factors than a consideration of *P. extincta* alone has been able to. Further insights into the ecology of other land snail species may also enhance our ability to model palaeoenvironments via excavated fossil land snail shells.

Although good long-term data from ecological and biological information is available on *P. extincta* shells, there is still a need to refine our understanding of this species. In particular, *P. extincta* deposition rates before and after 3,100 BP raise more questions than answered here; further sediment analyses may clarify some of these questions. Similarly, the changes in *P. extincta* shell characteristics documented here may indicate changes in human and climatic impacts on sedimentation rates within caves. Further attempts should be made to determine the influence of human activities on ecosystems within the Mitchell-Palmer region, and how people may have adjusted to environmental change in the past.

In recognising the ability of vegetation to accommodate to changes in certain environmental variables, it is probable that the Chillagoe Formation vine thickets are now remnants of a more extensive Pleistocene-early Holocene flora, now represented as permanent refugia. In this sense, *P. extincta* highlights the relevance of, and promotes the need for, knowledge of scales of biotic changes in the recent past and for 'dynamic' conservation strategies to accommodate these.

In short, the main value of this work is that the land snail data point to a reasonable but limited degree of variability in palaeoenvironmental change for hitherto unstudied parts of north Queensland. In particular, it questions the exact applicability of the Atherton curves to inland regions, while at the same time supporting established trend directions. The use of *P. extincta* in this project indicates that land snails represent a significant and new potential source of data for Australian palaeoecological studies.

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#### LITERATURE CITED

- AHARON, P. 1983. Surface ocean temperature variations during the late Wisconsin stage:  $^{16}\text{O}/^{18}\text{O}$  isotopic evidence from Papua New Guinea. Pp. 3-4. In Chappell, J. & Grindrod, J. (eds) CLIMANZ: Proceedings of First CLIMANZ, February 1981, Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- ALLEN, M.J. 1991. Analysing the landscape: a geographical approach to archaeological problems. Pp. 37-54. In Schofield, A.J. (ed.) Interpreting artefact scatters: contributions to ploughzone archaeology, (Oxbow Books: Oxford).
1992. Environment and landuse: the economic development of the community who built Stonehenge (an economy to support the stones). Proceedings of the British Academy 92: 115-144.
1994. The land-use history of the southern English Chalklands with an evaluation of the Beaker Period using environmental data: colluvial deposits as environmental and cultural indicators. Unpubl. PhD thesis, University of Southampton, Southampton.
- 1995a. Land molluscs. Pp. 92-100. In Wainwright, G.J. & Davies, S.M. (eds) Barksbury Camp, Hampshire: excavations 1973 and 1981. English Heritage Archaeological Report 4. (English Heritage: London).
- 1995b. The prehistoric land-use and human ecology of the Malling-Caburn Downs: two late Neolithic/Early Bronze Age sites beneath colluvium. Sussex Archaeological Collections 133: 19-43.
1997. Environment and land-use: the economic development of the communities who built Stonehenge (an economy to support stones). Pp. 115-144. In Cunliffe, B.W. & Renfrew, A.C. (eds) Science and Stonehenge. Proceedings of the British Academy 92.
- In press. High resolution mapping in Neolithic and Bronze Age landscapes and land-use: the combination of multiple palaeo-environmental analysis and topographic modelling. In Fairbairn, A. (ed.) Landscape and environment, economy and society: plants in Neolithic Britain. (Oxbow Books: Oxford).
- ALLEN, M.J., MORRIS, M. & CLARK, R.H. 1995. Food for the living: a reassessment of a Bronze Age barrow at Bucksdon, Basingstoke, Hampshire. Proceedings of the Prehistoric Society 61: 157-189.
- ALLEN, M.J. & WYLES, S. 1993. The landuse history: the molluscan evidence. Pp. 45-50. In Graham, A. & Newman, C. (eds) Recent excavations of Iron Age and Romano-British enclosures in the Avon Valley, Wiltshire. Wiltshire Archaeology and Natural History Magazine 86: 8-57.
- BELL, F.C., WINTER, J.W., PAHL, L.I. & ANDERSON, R.G. 1987. Distribution, area and tenure of rainforest in northeastern Australia. Proceedings of the Royal Society of Queensland 98: 27-39.
- BENGSTON, S.A., NILSSON, A., NORDSTROM, S. & RUNDGREN, S. 1979. Selection for adult shell size in natural populations of the landsnail *Cepaea hortensis* (Muller). Annales Zoologici Fennici 16: 187-194.
- BISHOP, M.J. 1981. The biogeography and evolution of Australian land snails. Pp. 924-954. In Keast, A. (ed.) Ecological biogeography of Australia. (Dr W. Junk: The Hague).
- BOWLER, J. 1983. 18±2KA: northern Australia hydrologic evidence. Pp. 47-48. In Chappell, J. & Grindrod, J. (eds) CLIMANZ: Proceedings of First CLIMANZ, February 1981. Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- BUTLER, D. 1998. Environmental change in the Quaternary. Pp. 78-97. In David, B. (ed.) Ngarrabullgan: geographical investigations in Djungan Country, Cape York Peninsula. Monash Publications in Geography and Environmental Science 51. (Monash University, Clayton).
- CARNAHAN, J.A. 1989. Australia: present vegetation (map). (Australian Surveying and Land Information Group, Dept. of Administrative Services: Canberra).
- CARTER, S.P. 1990. The stratification and taphonomy of shells in calcareous soils: implications for land snail analysis in archaeology. Journal of Archaeological Science 17: 495-508.
- CHAPPELL, J. 1982. Sea levels and sediments: some features of the context of coastal archaeological sites in the tropics. Archaeology in Oceania 17: 69-78.
- CHAPPELL, J., CHIVAS, A., WALLENSKY, E., POLACH, H. & AHARON, P. 1983. Holocene palaeoenvironmental changes, central to north Great Barrier Reef inner zone. Bureau of Mineral Resources Journal of Geology and Geophysics 8: 223-235.
- CHILLAGOE CAVING CLUB 1982. Chillagoe karst: a speleological field guide to the towers and caves of the Chillagoe-Mungana-Rookwood areas in Far North Queensland, Australia. (Chillagoe Caving Club: Cairns).
1988. Mitchell-Palmer karst: a speleological field guide for the towers and caves of the Mitchell-Palmer areas in Far North Queensland, Australia. (Chillagoe Caving Club: Cairns).
1990. Chillagoe karst: a speleological field guide to the towers and caves of the Chillagoe-Mungana-Rookwood areas in Far North Queensland, Australia. Supplement Number 2. (Chillagoe Caving Club: Cairns).

- CLEAL, R.M.J. & ALLEN, M.J. 1994. Investigation of tree-damaged barrows on King Barrow Ridge and Luxenborough Plantation, Amesbury. Wiltshire Archaeological and Natural History Magazine 87: 54-84.
- CONNAH, G. & McMILLAN, N.F. 1964. Snails and archaeology. *Antiquity* 38: 62-64.
- DAVID, B. & CHANT, D. 1995. Rock Art and regionalisation in North Queensland prehistory. *Memoirs of the Queensland Museum* 37: 357-528.
- DAVID, B. & LOURANDOS, H. 1997. 37,000 years and more in tropical Australia: investigating long-term archaeological trends in Cape York Peninsula. *Proceedings of the Prehistoric Society* 63: 1-23.
- DAVID, B. & STANISIC, J. 1991. Land snails in Australian archaeology: initial results from Echidna's Rest (north Queensland). *The Artefact* 14: 19-24.
- EVANS, J.G. 1969. Land and freshwater Mollusca in archaeology: chronological aspects. *World Archaeology* 1: 170-183.
- 1971a. Habitat change on the calcareous solid of Britain: the impact of Neolithic man. Pp. 27-73. In Simpson, D.D.A. (ed.) *Economy and settlement in Neolithic and early Bronze Age Britain and Europe*. (Leicester University Press: Leicester).
- 1971b. Notes on the environment of early farming communities in Britain. Pp. 11-26. In Simpson, D.D.A. (ed.) *Economy and settlement in Neolithic and early Bronze Age Britain and Europe*. (Leicester University Press: Leicester).
1972. Land snails in archaeology. (Seminar Press: London).
- FENSHAM, R.J. 1995. Floristics and environmental relations of inland dry rainforests in north Queensland, Australia. *Journal of Biogeography* 22: 1047-1063.
1996. Land clearance and conservation of inland dry rainforest in north Queensland, Australia. *Biological Conservation* 75: 289-298.
- GALLOWAY, R.W. & KEMP, E.M. 1981. Late Cainozoic environments in Australia. Pp. 52-80. In Keast, A. (ed.) *Ecological biogeography of Australia*. (Dr W. Junk: The Hague).
- GALLOWAY, R.W., GUNN, R.H. & STONY, R. 1970. Lands of the Mitchell-Normanby Area. CSIRO Land Research Series 26. (CSIRO: Canberra).
- GILLISON, A.N. 1987. The dry rainforests of Terra Australis. Pp. 305-321. In Werren, G. & Kershaw, A.P. (eds) *The Rainforest Legacy: Australian National Rainforest Survey, Vol. 1*. (Australian Government Publishing Service: Canberra).
- GOODFRIEND, G.A. 1986. Variation in land-snail shell form and size and its causes: a review. *Systematic Zoology* 35: 204-223.
1992. The use of land snails in palaeoenvironmental reconstruction. *Quaternary Science Reviews* 11: 665-685.
- GOULD, S.J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: a way of studying nonadaptation. *Systematic Zoology* 33: 217-237.
- HEAD, L. & STUART, I-M.F. 1980. Change in the Aire: Palaeoecology and prehistory in the Aire Basin, southwestern Victoria. *Monash Publications in Geography* 24. (Monash University: Clayton).
- HISCOCK, P. 1984. Preliminary report on the stone artefacts from Colless Creek Cave, northwestern Queensland. *Queensland Archaeological Research* 1: 120-151.
- HISCOCK, P. & KERSHAW, A.P. 1992. Palaeoenvironments and prehistory of Australia's tropical Top End. Pp. 43-75. In Dodson, J. (ed.) *The Naive Lands: Prehistory and environmental change in Australia and the southwest Pacific*. (Longman Cheshire: Melbourne).
- HOPKINS, M.S., ASH, J., GRAHAM, A.W., HEAD, J. & HEWETT, R.K. 1993. Charcoal evidence of the spatial extent of the *Eucalyptus* woodland expansions and rainforest contractions in north Queensland. *Journal of Biogeography* 20: 357-372.
- HOPLEY, D. 1983. Evidence of 15,000 years of sea level change in tropical Queensland. Pp. 93-104. In Hopley, D. (ed.) *Australian sea levels in the last 15,000 years: a review*. Occasional Paper 3. (Dept. of Geography, James Cook University of North Queensland: Townsville).
- HUGHES, P. 1983. Colless Creek rockshelter archaeological site, NW Queensland, 18KA. Pp. 59-61. In Chappell, J. & Grindrod, J. (eds) *CLIMANZ: Proceedings of First CLIMANZ, February 1981*. Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- IREDALE, T. 1937. A basic list of the land Mollusca of Australia. Part II. *Australian Zoologist* 9: 1-39.
1938. A basic list of land Mollusca of Australia. Part III. *Australian Zoologist* 9: 83-124.
- JENNINGS, J.N. 1985. *Karst geomorphology*. (Basil Blackwell: Oxford).
- KAHN, T.P. & LAWRIE, B.C. 1987. Vine thickets of the inland Townsville region. Pp. 159-201. In Werren, G. & Kershaw, A.P. (eds) *The Rainforest Legacy: Australian National Rainforest Survey, Vol. 1*. (Australian Government Publishing Service: Canberra).
- KEMP, E.M. 1981. Tertiary Palaeogeography and the evolution of the Australian climate. Pp. 32-49. In Keast, A. (ed.) *Ecological biogeography of Australia*. (Dr W. Junk: The Hague).
- KENNARD, A.S. 1897. The post Pliocene non-marine Mollusca of Essex. *Essex Nature* 10: 87-109.
- KERSHAW, A.P. 1970. A pollen diagram from Lake Euramoo, north-east Queensland, Australia. *New Phytologist* 69: 785-805.

1971. A pollen diagram from Quinean Crater, north-east Queensland, Australia. *New Phytolith* 70: 669-681.
1974. A long continuous pollen sequence from north-eastern Australia. *Nature* 251: 222-223.
1975. Late Quaternary vegetation and climate in north-eastern Australia. Pp. 181-187. In Suggate, R.P. & Creswell, M.M. (eds) *Quaternary Studies*. (Royal Society of New Zealand: Wellington).
1976. A late Pleistocene and Holocene pollen diagram from Lynch's Crater, north-eastern Queensland, Australia. *New Phytolith* 77: 469-498.
1985. An extended late Quaternary vegetation record from north-eastern Queensland and its implications for the seasonal tropics of Australia. *Proceedings of the Ecological Society of Australia* 13: 179-189.
1986. Climatic change and Aboriginal burning in north-east Australia during the last two glacial/interglacial cycles. *Nature* 322: 47-49.
1994. Pleistocene vegetation of the humid tropics of northeastern Queensland, Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* 109: 339-412.
- KERSHAW, A.P., McKENZIE, G.M. & McMINN, A. 1993. A Quaternary vegetation history of northeastern Queensland from pollen analysis of ODP site 820. In McKenzie, J.A., Davic, P.J. & Palmer-Johnson, A. (eds) *Proceedings of the Ocean Drilling Program, Scientific Results* 133: 107-114.
- KERSHAW, A.P., QUILTY, P.G., DAVID, B., VAN HUET, S. & McMINN, A. 2000. Palaeobiogeography of the Quaternary of Australasia. *Memoir of the Association of Australasian Palaeontologists* 23: 471-516.
- LAMB, L. 1996. Investigating changing stone technologies, site use and occupational intensities at Fern Cave, north Queensland. *Australian Archaeology* 42: 1-7.
- LEES, B.G., YU, Y. & PRICE, D.M. 1992. Thermoluminescence dating of dunes at Cape St. Lambert, East Kimberley, northern Australia. *Marine Geology* 106: 131-139.
- LOWE, J.J. & WALKER, M.J.C. 1984. *Reconstructing Quaternary environments*. (Longman: London).
- McGLONE, M.S., KERSHAW, A.P. & MARKGRAF, V. 1992. El Niño/Southern Oscillation climatic variability in Australasian and South American palaeoenvironmental records. Pp. 435-462. In Diaz, H.F. & Markgraf, V. (eds) *El Niño: historical and palaeoclimatic aspects of Southern Oscillation*. (Cambridge University Press: Cambridge).
- NIX, A. & KALMA, J.D. 1972. Climate as a dominant control in the biogeography of northern Australia and New Guinea. Pp. 61-92. In Walker, D. (ed.) *Bridge and barrier: the natural and cultural history of Torres Strait*, pp. Dept. Biogeography and Geomorphology, R.S.Pac.S. (Australian National University: Canberra).
- O'CONNER, T. 1988. Slums, puddles and ditches: are molluscs useful indicators. Pp. 61-68. In Murphy, P. & French, C. (eds) *The exploration of wetlands*. (British Archaeological Reports 186: Oxford).
- ODHNER, N. 1917. Results of Dr E.Mjöberg's Swedish Scientific Expeditions to Australia 1910-1913. XVII. Mollusca. *Kungliga Svenska Vetenskapsakademiens Handlingar* 52: 1-115.
- OWEN, D.T. 1965. A population study of an equatorial land snail, *Limnicolaria martensiana* (Achatinidae). *Proceedings of the Zoological Society of London* 144: 361-382.
- POKRYSZKO, B.M. 1996. The Gastrocoptinae of Australia (Gastropoda: Pulmonata: Pupilloidea): Systematics, distribution, and origin. *Invertebrate Taxonomy* 10: 1085-1150.
- PORCH, N. In press. Palaeoenvironmental interpretation of late Quaternary non-marine mollusc assemblages from Pulbeena Swamp, northwestern Tasmania. *Alcheringa*.
- PORCH, N. & ALLEN, J. IN PREP. A 35,000 year land snail and vertebrate sequence from Wareen Cave, a late Pleistocene archaeological site in southwest Tasmania. To be submitted to *Journal of Archaeological Science*.
- ROBINSON, T.W.L. 1982. Limestone solution experiment at Chillagoe. *Tower Karst* 4: 71-76.
- ROBINSON, M. 1988. Molluscan evidence for pasture and meadowland on the floodplain of the upper Thames basin. Pp. 101-112. In Murphy, P. & French, C. (eds) *The exploitation of the wetlands*. (British Archaeological Reports, British Series 186: Oxford).
- SCAIFE, R.G. 1995. Boreal and Sub-boreal chalk landscape: pollen evidence. Pp. 51-55. In Cleal, R.M.J., Walker, K.E & Montague, R. (eds) *Stonehenge in its landscape; the twentieth century excavations*. (English Heritage Archaeological Report 10: London).
- SHARPLES, N.M. 1991. Maiden Castle: excavations and field survey 1985-6. (English Heritage Archaeological Report 19: London).
- SHULMEISTER, J. & LEES, B.G. 1995. Pollen evidence from tropical Australia for the onset of an ENSO dominated climate at c.4000 BP. *The Holocene* 5(1): 10-18.
- SINGH, G., KERSHAW, A.P. & CLARK, R. 1981. Quaternary vegetation and fire history in Australia. Pp. 23-54. In Gill, A.M., Groves, R.H. & Noble, I.R. (eds) *Fire and the Australian biota*. (Australian Academy of Science: Canberra).
- SMITH, B.J. 1992. Non-marine Mollusca. Pp. 1-405. In Houston, W.W.K. (ed.) *Zoological Catalogue of Australia*. Australian Government Publishing Service: Canberra).
- SMITH, B.J. & KERSHAW, R.C. 1979. *Field guide to the non-marine molluscs of South Eastern*



- Australia. (Australian National University Press: Canberra).
1981. Tasmanian land and freshwater molluscs. Fauna of Tasmania Handbook Series. No. 5. (University of Tasmania: Hobart).
- SMITH, B.J. & STANISIC, J. 1998. Pulmonata: Introduction. Pp. 1037-1061. In Beesley, P.L., Ross, G.J.B. & Wells, A. (eds) Mollusca: the southern synthesis. Fauna of Australia 5B. (CSIRO Publishing: Melbourne).
- SOLEM, A. 1972. Mollusks from prehistoric sites in Afghanistan. Transactions of the American Philosophical Society 62: 57-65.
1974. The shell makers: introducing Mollusks. (John Wiley & Sons: New York).
1976. Endodontoid land snails from Pacific Islands. Part I. Family Endodontidae. Fieldiana: Zoology, Special Publication pp. 1-508.
1982. Small land snails from northern Australia. II. Species of *Westracystis* Iredale, 1939 (Mollusca: Pulmonata, Helicarionidae). Journal of the Malacological Society of Australia 5: 175-193.
1984. Small land snails from Northern Australia. III: Species of Helicodiscidae and Charopidae. Journal of the Malacological Society of Australia 6: 155-179.
1988. Maximum in the minimum: biogeography of land snails from the Ningbing Ranges and Jeremiah Hills, north-east Kimberley, Western Australia. Journal of the Malacological Society of Australia 9: 59-113.
1991. Land snails of the Kimberley rainforest patches and biogeography of all Kimberley land snails. Pp. 145-246. In McKenzie, N.L., Johnston, R.B. & Kendrick, P.G. (eds) Kimberley rainforests of Australia. (Surrey Beatty & Sons: Chipping Norton).
- 1992a. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Part 1. Systematics, distribution and variation. Records of the South Australian Museum, Monograph Series 2: 1-338.
- 1992b. Camaenid land snails from southern and eastern South Australia, excluding Kangaroo Island. Part 2. Biogeography and covariation. Records of the South Australian Museum, Monograph Series 2: 339-424.
- SOLEM, A. & CHRISTENSEN, C.C. 1984. Camaenid land snail reproductive cycle and growth patterns in semiarid areas of north-western Australia. Australian Journal of Zoology 32: 471-491.
- SPARKS, B.W. 1969. Non-marine Mollusca and archaeology. Pp. 395-406. In Brothwell, D. & Higgs, E. (eds) Science in Archaeology. (Thames & Hudson: London).
- STANISIC, J. 1990. Systematics and biogeography of eastern Australian Charopidae (Mollusca, Pulmonata) from subtropical rainforests. Memoirs of the Queensland Museum 30(1): 1-238.
- 1994a. The distribution and patterns of species diversity of land snails in eastern Australia. Memoirs of the Queensland Museum 36(1): 207-214.
- 1994b. Landsnails of the Wet Tropics biogeographic region, northeastern Queensland. Australian Shell News 87 (October): 1-2.
- 1997a. Land snail diversity in Queensland: an overview. Part 1. Australasian Shell News 94: 6.
- 1997b. Land snail diversity in Queensland: an overview. Part 2. Australasian Shell News 95: 6.
- 1997c. An area of exceptional land snail diversity: the Macleay Valley, northeastern New South Wales. Memoirs of the Museum of Victoria 56: 441-448.
- 1997d. Land snails of the Chillagoe limestones. Australasian Shell News 96: 3-6.
1998. A survey of the land snails of the land snails of the Queensland Brigalow Lands: Their distribution, conservation status and close association with vine thickets. Unpublished report to the Queensland Department of Environment (Queensland Museum: Brisbane).
1999. Land snails and dry vine thickets in Queensland: using museum invertebrate collections in conservation. Pp. 257-263. In Ponder, W. & Lunney, D. (eds) The other 99%. The conservation and biodiversity of invertebrates. Transactions of the Royal Zoological Society of New South Wales. (Surrey Beatty & Sons: Chipping Norton).
- STANISIC, J. & INGRAM, G.J. 1998. Sandstone, snails and slaters: Pp. 112-118. In David, B. (ed.) Ngarrabullgan: geographical investigations in Djungan Country, Cape York Peninsula' Monash Publications in Geography and Environmental Science, Number 51. (Monash University: Melbourne).
- STANISIC, J., EDDIE, C., HILL, A. & POTTER, D. 1994. A preliminary report on the distribution of land snails occurring within the Wet Tropics area. Unpubl. report to the Wet Tropics Management Authority. (Queensland Museum: Brisbane).
- STEPHANS, K. & L. HEAD, L. 1995. Palaeoecology of archaeological and swamp sites in SE Cape York Peninsula. Pp. 18-32. In Morwood, M. & Hobbs, D.R. (eds) Quinkan prehistory: the archaeology of Aboriginal art in southeast Cape York Peninsula, Australia. (Tempus 3. University of Queensland: St. Lucia).
- TILLIER, S. 1981. Clines, convergence and character displacement in New Caledonian diplommatinids (land prosobranchs). Malacologia 21: 177-208.
- TORGENSEN, T., LULY, J., DE DECKKER, P., JONES, M.R., SEARLE, D.E., CHIVAS, A.R. & ULLMAN, W.J. 1988. Late Quaternary environments of the Carpentaria Basin, Australia. Palaeogeography, Palaeoclimatology, Palaeoecology 67: 245-261.
- WAINWRIGHT, G.J. & DAVIES, S.M. 1995. Balksbury Camp, Hampshire: Excavations 1973

- and 1981. English Heritage Archaeological Report 4. (English Heritage: London).
- WEBB, L.J. & TRACEY, J.G. 1981. Australian rainforests: patterns and change. Pp. 605-694. In A. Keast, A. (ed.) Ecological biogeography of Australia. (Dr W. Junk: The Hague).
- WINTER, J.W., BELL, F.C., PAHL, L.L. & ATIERTON, R.G. 1987. The distribution of rainforest in north-eastern Queensland. Pp 223-227. In Werren, G. & Kershaw, A.P. (eds) The Rainforest Legacy: Australian National Rainforest Survey, Vol. 1. (Australian Government Publishing Service: Canberra).
- WOODWARD, B.B. 1908. Notes on the drift and underlying deposits at Newquay, Cornwall. *Geology Magazine* V (5): 10-18, 80-87.

## APPENDIX 1

Locality data for *P. extincta* from Mitchell-Palmer area. (QM reg. no., locality and habitat data, latitude/longitude).

- MO22998, Laura-Palmerville Rd, N of Palmerville, 15°48'45"S, 144°03'46"E
- MO23375, Laura-Palmerville Rd, N of Palmerville, 15°53'20"S, 144°05'20"E
- MO61172, Limestone Ck Rd, SSE of Palmerville, 16°02'36"S, 144°07'32"E
- MO61191, Limestone Ck Rd, SSE of Palmerville, 16°02'51"S, 144°08'28"E
- MO23592, Limestone Ck Rd, SSE of Palmerville, 16°02'53"S, 144°07'23"E
- MO61205, Limestone Ck Rd, SSE of Palmerville, 16°03'13"S, 144°08'24"E
- MO61156, Limestone Ck Rd, SSE of Palmerville, 16°03'22"S, 144°07'39"E
- MO23584, Limestone Ck Rd, SSE of Palmerville, 16°07'33"S, 144°08'47"E
- MO23388, Limestone Ck Rd, SSE of Palmerville, 16°08'58"S, 144°09'07"E

Locality data for *P. extincta* from Chillagoe-Mungana area. (QM reg. no., locality and habitat data, latitude/longitude).

- MO15955, Marachoo Cave, 17°05'39"S, 144°23'28"E
- MO25996, Carpentaria Cave, 17°05'46"S, 144°23'56"E
- MO50231, Capricorn Cave, 17°06'15"S, 144°24'36"E
- MO53325, Chillagoe, c.13km WNW on Chillagoe-Mungana Rd, 17°06'15"S, 144°23'40"E
- MO58485, Chillagoe, c.10km WNW on Chillagoe-Mungana Rd, 17°06'45"S, 144°24'55"E
- MO53335, Chillagoe, c.10km WNW on Chillagoe-Mungana Rd, 17°06'45"S, 144°24'55"E
- MO53551, Chillagoe, c.3km N on road to Metal Hills, 17°07'20"S, 144°31'10"E
- MO19527, Spring Cave, 17°08'03"S, 144°25'30"E
- MO50229, Tea Tree Cave, 17°10'33"S, 144°08'18"E
- MO53448, Chillagoe, c.3km SW on road to Royal Arch Caves, 17°10'35"S, 144°00'15"E
- MO58540, Chillagoe, c.3km SW on road to Royal Arch Caves, 17°10'35"S, 144°00'15"E
- MO53436, Chillagoe, c.6km SW at Royal Arch Caves, 17°11'15"S, 144°30'00"E
- MO38499, Chillagoe, c.8km SE on road to Almaden, 17°11'20"S, 144°33'05"E
- MO53564, Chillagoe, c.8km SE on road to Almaden, 17°11'20"S, 144°33'05"E
- MO58547, Chillagoe, c.8km SE on road to Almaden, 17°11'20"S, 144°33'05"E